

MADROÑO

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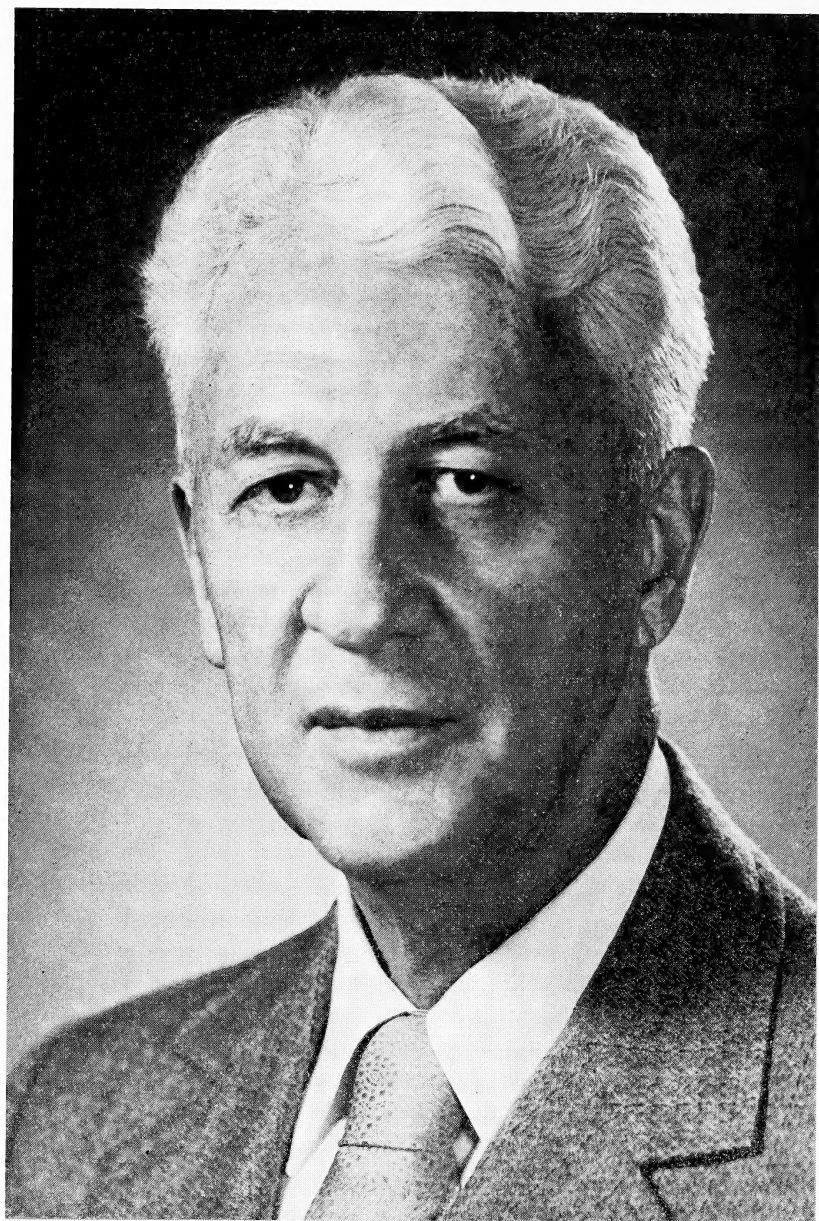
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Volume 22 of Madroño is dedicated to Lyman Benson, Professor of Botany, Pomona College, Claremont, California, in recognition of his contributions to western American botany, particularly his studies on *Ranunculus* and cacti and his dedication to teaching.

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ANALYSIS OF A PROGENY TEST OF A HYBRID OAK, *QUERCUS GAMBELII* × *Q. TURBINELLA*

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Natural hybrids between *Quercus gambelii* Nutt. and *Q. turbinella* Greene (figs. 1–3) are known from numerous locations in Utah and Arizona (Cottam, Tucker, and Drobnick, 1959; Tucker, Cottam, and Drobnick, 1961). They commonly occur in northern Arizona and southern Utah, where the parental species are sympatric, but many have also been found farther north in Utah beyond the northern limits of *Q. turbinella*. Indeed, the most northerly hybrid location is some 260 miles beyond the present northern limits of *Q. turbinella*. This anomalous situation seems to be best explained by the hypothesis that the range of *Q. turbinella* extended farther north at some time in the past, the most likely time being the post-Pleistocene Altithermal period. This period, which extended from about 7500 to 4000 years ago, was marked by a warmer climate than at present; this would have provided the necessary environmental conditions for the northward migration of *Q. turbinella*. As the climate subsequently became cooler, *Q. turbinella* was eliminated in these northern areas but not before it had produced numerous hybrids with the common, widespread *Q. gambelii*. Many of these hybrids have persisted to the present time (see Cottam et al., 1959).

In a detailed analysis of these field hybrids (Tucker et al., 1961), morphological intermediacy was taken as proof of their hybridity. It was acknowledged that direct genetic evidence would also be desirable, and it was mentioned that progeny tests were in progress (Tucker et al., 1961, p. 332). Another procedure, of course, would have been experimental synthesis of the hybrid by crossing the two presumed parents. Both procedures have now been successfully pursued. Cottam and Drobnick have experimentally crossed *Q. gambelii* and *Q. turbinella* several times (unpubl. data), with the resulting hybrids differing in no significant morphological detail from the natural hybrids. Our paper reports the results of a progeny test performed with a large collection of acorns from a single natural hybrid in Utah.

The parent hybrid is a large shrub growing in Coon Canyon in the Oquirrh Mountains, Salt Lake County, Utah. It was discovered by Rudy Drobnick in the course of a M.S. study at the University of Utah. Here, at an elevation of 5300 feet, on a south exposure, it was surrounded by shrubs of *Q. gambelii*. In 1957 it bore a heavy crop of acorns, and on September 10, 1957, a large collection (*Drobnick 10*,



FIG. 1-3. 1, Representative specimen of *Quercus gambelii* (Tucker 2826-9); 2, specimen from the hybrid, *Q. gambelii* \times *Q. turbinella*, Oquirrh Mountains, Salt Lake County, Utah (Drobnick 10-1); 3, representative specimen of *Q. turbinella* (Tucker 2810-1).

which included a voucher specimen, now on file at U.C., Davis, fig. 2) was made and sent to the senior author. The acorns were quite variable in size, and it was thought that the smaller ones might have less fully developed embryos than the larger ones; but there was also a possibility that the smaller ones might represent individuals closer to *Q. turbinella* (for the latter species has smaller acorns and smaller embryos than *Q. gambelii*). Therefore, rather than run the risk of biasing our results by rejecting them, the small acorns were sown in roughly the same proportion as their occurrence in the sample as a whole.

As a secondary experiment, groups of 100 of the larger acorns and 100 of the smaller ones were sown under comparable conditions. A somewhat higher percentage of the larger germinated, 83 compared to 68 of the smaller ones. Although this was inconclusive evidence, it tended to strengthen our suspicion that the smaller acorns might be "weaklings", containing less fully developed embryos.

Altogether, 900 acorns were sown. A total of 708 seedlings was obtained, but by March 24, 1958, the number had diminished to 522. These were planted out in a plot in the University Arboretum during the spring of that year. The project was terminated after seven growing seasons, and on August 26 and 27, 1964, the individual heights of the 183 survivors were measured and a voucher specimen collected from each.

Over the period of this progeny test, conspicuous variation in size and general vigor had become apparent. At the termination of the project, the hybrids ranged from moribund dwarfs a few centimeters in height to vigorous, freely branching individuals well over two meters tall. In gross morphology, also (notably size, form, and color of the leaves), the hybrids were extremely variable. Those with the smallest leaves closely approached the maternal parent. It was interesting that none was noticeably more *turbinella*-like than the parental hybrid, i.e., none had leaves that were noticeably paler in color, less deeply lobed, or more spinose. Instead, the great majority were more suggestive of *Q. gambelii*, and several individuals would have been readily identified as this species (fig. 4). Indeed, the whole aspect of the group indicated a backcross generation to *Q. gambelii*.

Although there was a high rate of attrition in the progeny (522 planted out in 1958; only 183 survivors in 1964), it seems quite unlikely that the absence of any *turbinella*-like individuals was due to a higher mortality rate among them than among the *gambelii*-like individuals. Indeed, if there had been differential survival (and there may have been), any *turbinella*-like individuals should have been better adapted to the hot, dry summers of the Sacramento Valley than the more *gambelii*-like individuals.

Analysis of the progeny. Individuals in the progeny were analyzed (by Bogert) using the same procedures as in the study of the natural



FIG. 4. Leaves from selected individuals in the hybrid progeny (a single representative leaf taken from each). This small sample of the progeny shows the range of leaf forms, from the largest and most *gambelii*-like, to the smallest, and most like the maternal parent. The greater part of the progeny, however, had leaves more similar to one form or another in the two middle rows.

hybrids (Tucker et al., 1961). The characters analyzed were: (1) leaf length, (2) relative depth of lobing (vein:lobe ratio), (3) mean number of rays per stellate hair, (4) leaf color, (5) apex of marginal teeth or lobes, and (6) density of twig pubescence. The data from our analysis are presented as a frequency histogram (fig. 5) using Anderson's (1936) hybrid index method. Every specimen was scored on each of the six characters stated above. The condition typical of *Q. turbinella* was given a score of zero, that of *Q. gambelii* a score of two, and an intermediate condition of a score of one. The quantitative characters (No. 1, 2, and 3, of the six mentioned above) were scored according to the following scheme:

Character	<i>Q. turbinella</i> (score: 0)	Intermediate (score: 1)	<i>Q. gambelii</i> (score: 2)
leaf length	36 mm or less	37-63 mm	64 mm or more
vein:lobe ratio	2.41 or more	1.75-2.40	1.74 or less
mean ray no. per stellate hair	8.0 or more	4.1-7.9	4.0 or less

The qualitative characters (No. 4, 5, and 6) were judged using the same "standard specimens" (with one exception) that were used in the study by Tucker et al. (1961). The total score possible would thus range from zero (for an individual scored as *turbinella* on all six characters) to twelve (for an individual scored as *gambelii* on all six).

The resulting index totals for the hybrid progeny are presented in Figure 5. Presented for comparison are similar index totals for population samples of *Q. turbinella* and *Q. gambelii*. These are the same collections from which the data were included as pictorialized scatter diagrams in the study by Tucker et al. (1961, fig. 3, 4).

It is evident that the points regarding the nature of the progeny deduced from inspection of gross morphology, mentioned previously, are borne out by our analysis. The great majority of the progeny tends to be more *gambelii*-like than the maternal parent (the original hybrid in the Oquirrh mountains), and only four in the entire progeny had index totals as low as its total (7). Assuming that the mean hybrid index value of a backcross progeny would be midway between that of the F_1 (7) and the score for pure *Q. gambelii* (12), we would thus expect a value of 9.5. The actual mean of the progeny was 9.7, a value very close to expectation.

A breakdown of the number of individuals scored on each character as *gambelii*, as intermediate, and as *turbinella*, is given in Table 1. It is apparent that only one individual, on a single character (leaf length), was scored as *turbinella*.

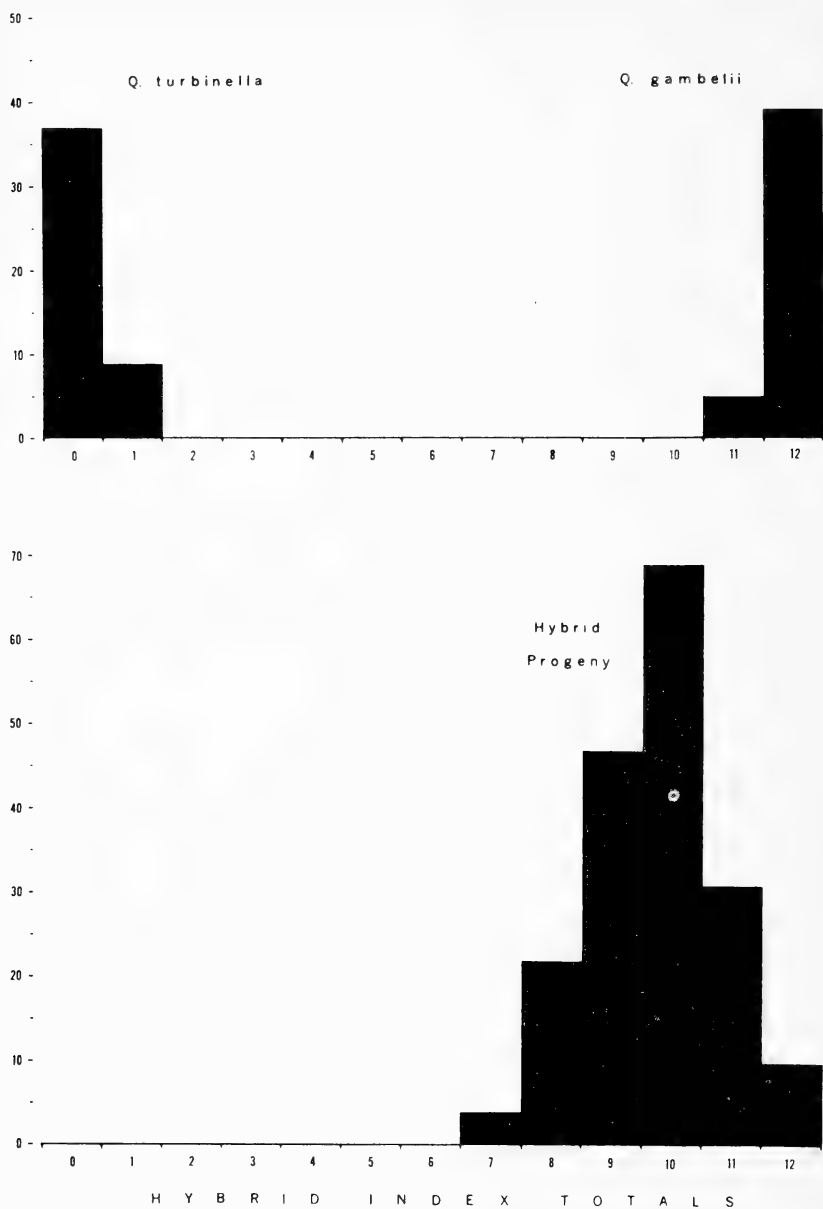


FIG. 5. Frequency histograms of hybrid index totals for (above) two combined population samples of *Q. turbinella* (Tucker 2810 and 2813) (left), and two combined population samples of *Q. gambelii* (Tucker 2775 and 2826) (right); and (below) the hybrid progeny. (Vertical scale at left indicates number of individuals.)

TABLE 1. CHARACTER ANALYSIS OF HYBRID PROGENY

Character	Scored as <i>gambelii</i>		Scored as intermediate		Scored as <i>turbinella</i>	
	No.	%	No.	%	No.	%
leaf length	(64 mm or more)		(37-63 mm)		(36 mm or less)	
	36	19.7	146	79.8	1	0.5
vein: lobe ratio	(1.74 or less)		(1.75-2.40)		(2.41 or more)	
	169	92.3	14	7.7	0	0
leaf color	84	45.9	99	54.1	0	0
lobe apex	144	78.7	39	21.3	0	0
twig pubescence	78	42.6	105	57.4	0	0
rays per stellate hair	(4.0 or less)		(4.1-7.9)		(8.0 or more)	
	170	92.9	13	7.1	0	0
Totals:	681	62.0	416	37.9	1	.1

Discussion and conclusions. There can be little doubt that the parent shrub in the Oquirrh Mountains was a hybrid. This is indicated not only by its morphological intermediacy, but also by the highly variable nature of the progeny, which at one extreme includes individuals very similar to the mother plant and at the other extreme a few individuals indistinguishable from *Q. gambelii*.

In a discussion of oak hybrids, Stebbins (1950, pp. 64-65) expressed the following views: "One interesting feature of the progeny of both artificial and natural oak hybrids is that in respect to vegetative characteristics they usually segregate so sharply that even among a relatively small number of individuals the parental types can be recovered (MacDougal 1907, Ness 1927, Coker and Totten 1934, Allard 1942, Wolf 1938, 1944, Yarnell 1933, and Stebbins, unpublished). This is in striking contrast to the behavior of interracial and interspecific hybrids in most other plant groups, in which the number of genetic factors controlling the differences between them is so large that it is relatively difficult to recover the parental types The evidence available suggests that the number of genes by which species of oaks differ from each other is considerably smaller than it is in the case of most other plant groups."

There are several points in the foregoing statement on which we would like to comment. First, the statement that vegetative characteristics usually segregate sharply is quite contrary to our experience. The senior author has yet to see a sizeable oak progeny that did not show a *graduated series* of forms from one extreme to the other. Indeed, of the oak studies cited by Stebbins, the only one that purports to show sharp character segregation was that of Yarnell (1933), but in our opinion, Yarnell's interpretation of his results is open to question. He analyzed

a single character (leaf size) in 20 second generation trees from seven F_1 's (that Ness, 1918, had originally produced by experimentally crossing *Quercus virginiana* and *Q. lyrata*). Yarnell's values show essentially a bimodal distribution. He referred to these second generation trees as " F_2 's", but when his study is carefully analyzed it seems much more likely that they were a composite of two backcross generations—one to each of the parental species, both of which were planted in the area (see Yarnell, 1933; also, Ness, 1918; 1927, p. 385). On this basis, a bimodal distribution would have been expected.

In the other oak studies cited by Stebbins, although the hybrid progenies were commonly referred to as " F_2 's", in most instances it is more likely that they were backcrosses. In all cases they were grown from acorns resulting from open pollination, with the source of the pollen unknown. Oak hybrids commonly occur as isolated F_1 trees growing with the parental species, and the progeny of an F_1 (when it is fertile) will usually result from backcrossing to one parent or the other, rather than from self-pollination (Palmer, 1948). Self-pollination experiments with oaks have usually indicated a moderate to high degree of self-incompatibility (Pjatnitskii, 1934; Wright, 1953; Schreiner, unpubl.).

In regard to the recovery of parental types in hybrid progenies, Anderson has pointed out (1949, pp. 25–26) that parental types may be expected to occur with higher frequency in a backcross generation than in an F_2 . As most authors have used the term, a "parental type" seems to be an individual resembling one parent quite closely, but that, one suspects, might show slight suggestions of the other parent when scrutinized very closely. In the oak studies cited by Stebbins, "parental types" were judged solely on leaf characters and did not include acorn, twig, or bud characters. Thus, such "parental types" were judged on the basis of very incomplete analyses, perhaps more so than in similar studies in other plant groups.

In any event, "parental types", as close approximations of the phenotype of the recurrent parent, do not seem to be particularly rare in first backcross progenies, as evidenced by studies in *Carthamus* (P. F. Knowles, pers. commun.), *Downingia* (Wood, 1961), *Geum* (Marsden-Jones, 1930), *Helianthus* (Long, 1966), *Phacelia* (Gillett, 1955), *Solidago* (Goodwin, 1937), and *Vernonia* (Jones, 1966). Therefore, the genus *Quercus* may not be as different from other plant groups as has been supposed.

Finally, to summarize briefly the results of this study, a progeny test was made with acorns from a natural hybrid of *Q. gambelii* \times *Q. turbinella* in the Oquirrh Mountains in Utah. The hybrid was growing with *Q. gambelii*, but not with *Q. turbinella*, which does not occur in that region. Seedlings of the progeny were analyzed on six morphological characters, which distinguish the parental species. The progeny showed great variation in all these characters, as well as in size and vigor. This

extreme variation in the progeny is corroborative evidence of the hybrid nature of the maternal parent; and the results of the analysis indicate that the progeny was probably a backcross to *Q. gambelii*.

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BULB MORPHOLOGY IN SOME WESTERN NORTH AMERICAN SPECIES OF ALLIUM

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The circumboreal genus *Allium* includes about 80 species in North America. Within this group nine well defined alliances are recognized (Ownbey and Aase, 1955; Saghir et al., 1966). This paper presents the results of a study of bulb morphology and seasonal development in the *Allium acuminatum* alliance and in selected species of the *A. falcifolium* and *A. kunthii* alliances. Numerous external bulb characters are used in the classification of *Allium* but little is known about their detailed morphology or development. In the only recent systematic study of bulb morphology, Mann (1960) demonstrated the naturalness of the European section *Molium* using comparative bulb morphology of six species in the section. Data presented here demonstrate that a very close relationship exists among species in the *A. acuminatum* alliance. They also support the observation, based on chromosome numbers, floral morphology, and other characters, that most of the New World species of *Allium* are closely related (Ownbey and Aase, 1955).

Members of the *Allium acuminatum* alliance have a generally uniform morphology, although major groups and subgroups are recognizable (McNeal, 1970). The alliance is marked by the strong sclerification of the inner epidermal cells of the inner leaf base. The cell walls become thickened, eventually forming a moisture retaining bulb coat with a characteristic pattern of cellular reticulation on its surface. Differences in the organization and development of the bulb allow recognition of two major species groups, one of which develops rhizomes while the other is non-rhizomatous.

In the rhizomatous group each bulb produces one to three rhizomes. A new bulb is borne terminally on each rhizome with the subsequent disappearance of the parent bulb. Within this group two subgroups are recognized; in the first, the rhizomes are short, not exceeding 2 cm in length, including the new bulbs. This subgroup includes *Allium bolanderi* Wats., *A. dictuon* St. John, and *A. mirabile* Hend. The second subgroup includes only *A. unifolium* Kell. with rhizomes up to 5 cm long. In the non-rhizomatous species of the alliance (*A. acuminatum* Hook., *A. amplexans* Torr., *A. crispum* Greene, *A. davisiae* Jones, *A. dichlamydeum* Greene, *A. hickmanii* Eastw., *A. hyalinum* Curran, *A. lacunosum* Wats., *A. peninsulare* Lemmon, *A. praecox* Bdg., and *A. serratum* Wats.), all

new growth occurs within the preceding year's bulb coats. All of these species have similar bulb morphology and no subgroups are recognized here.

The bulb morphology of *Allium acuminatum* was described by Mullen (1928). The present investigation confirms Mullen's work, extends it to include all of the non-rhizomatous species in the alliance, and compares the morphology of the rhizomatous and non-rhizomatous species. Because of their similar rhizomatous habit, two other species, *A. crenulatum* Wieg. of the *A. falcifolium* alliance, with short rhizomes, and *A. glandulosum* Link and Otto, of the *A. kunthii* alliance, with long rhizomes, were also examined.

MATERIALS AND METHODS

Representatives of all species of the *Allium acuminatum* alliance were collected in the western United States (Table 1) and cultivated either in the greenhouse or experimental garden at Pullman, Washington, or in the garden at Stockton, California. Their seasonal development was observed over a period of several years. Two methods were used to ascertain bulb structure and development; dissection of whole, live or preserved plants under a low power microscope and preparation of stained microsections from bulbs embedded in paraffin.

Material of *A. unifolium*, *A. bolanderi*, and *A. mirabile* was collected at 10 day intervals from 1 Jan. 1968 to 8 Apr. 1968 and again on 20 July 1968. Three other species, *A. dictyon*, *A. crenulatum*, and *A. glandulosum*, were collected after anthesis when the new bulbs were mature. The bulbs were killed in F.A.A. (formalin-acetic acid-alcohol), dehydrated through a tertiary butyl alcohol series, and embedded in paraffin using standard techniques (Johansen, 1940). Following embedding, serial sections, 10 microns thick were cut from each bulb. The sections were mounted on slides and stained in 0.1% solution of safranin in 50% alcohol for 18–24 hours and 0.2% solution of fast green in 95% alcohol for 5–10 seconds (Brooks, Bradley, and Anderson, 1963). Bulbs of all species were collected at various times and dissected while fresh or after preservation in F.A.A., or observed in the serial microsections to verify the structure and development sequences reported by Mullen.

RESULTS

A survey of all of the non-rhizomatous species of the *Allium acuminatum* alliance indicated no essential differences in their organizations or seasonal development. The following description is based on Mullen's 1928 study and on observations made during the present investigation.

Figure 1 is a diagram of a median-longitudinal section through a bulb of *Allium acuminatum*. It represents a bulb collected just after the resumption of growth in the early spring. The outer bulb coat, R, is a brown, yellow-brown, or gray, heavily sclerified resistant or protective

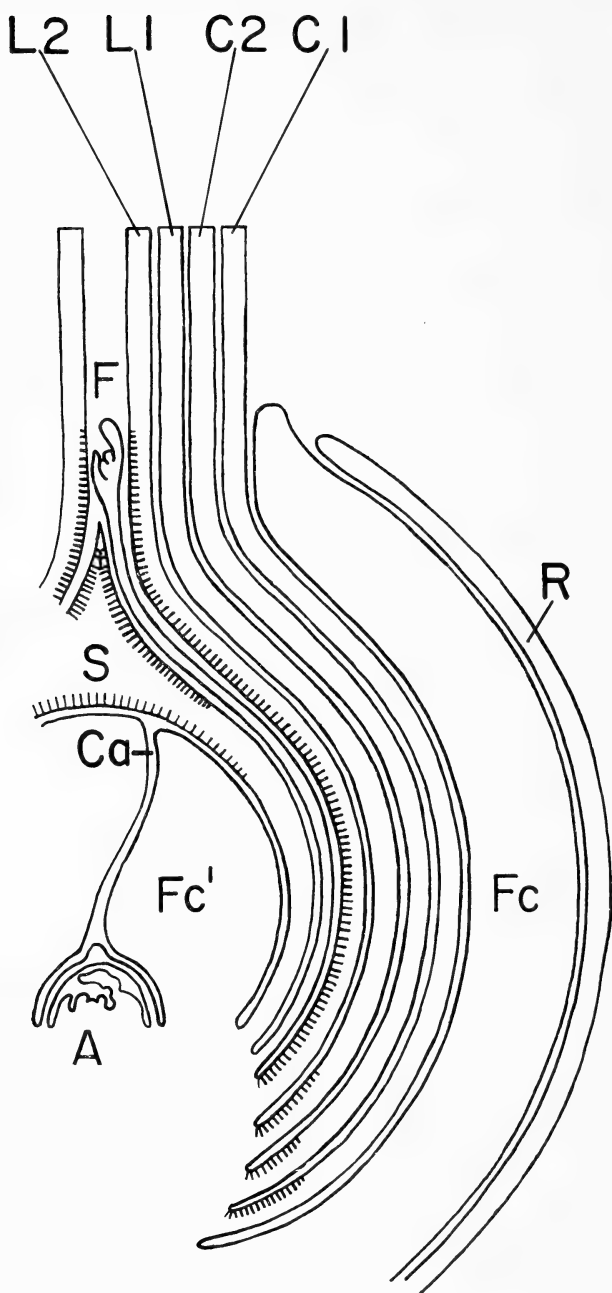


FIG. 1. Median-longitudinal section through the bulb of *Allium acuminatum* (After Mullen, 1928): A, apical meristem; Ca, canal; S, sheath; F, scape (current year); Fc', new fleshy cataphyll; Fc, old fleshy cataphyll; L1, L2, leaf bases; C1, C2, cataphyll bases; R, resistant layer.

layer. It was formed through the modification of the inner epidermis of the previous year's inner leaf base. This layer corresponds to the shaded portion of L2 in the diagram. It is all that remains of the foliar organs produced by the primary axis during the preceding growing season, the other leaf tissues having disintegrated in the intervening period. The resistant layer is one cell thick with the sclerified cell walls forming a characteristic reticulate pattern on the surface. The pattern depends on the size, shape, and arrangement of the epidermal cells forming the layer. (In *A. acuminatum*, for example, the cells are isodiametric, being either square or polygonal. In *A. crispum* they are elongate and rectangular in shape and arranged in vertical rows, so oriented as to give the appearance of a herringbone pattern; in *A. hyalinum*, on the other hand, the cells are elongate, but irregularly arranged and not forming any regular pattern.)

Not shown in Figure 1, but frequently observed in bulbs at this stage, is the dried basal portion of the previous year's scape. If present, it is located immediately inside the resistant layer, in a position corresponding to F in the present year's growth.

In *Allium*, as in almost all monocotyledonous plants, the inflorescence terminates the primary axis (Holttum, 1955). The *Allium* bulb is a highly condensed shoot on which the foliar organs arise from the apical meristem in an acropetal sequence. The scape develops immediately above the upper foliage leaf with a secondary axis forming below the scape in the axil of this leaf. Figure 1, then, represents this secondary axis that has developed into a new bulb, thus serving to continue the plant that produced it. Since the plant axis is composed of at least two branches, it is a sympodium. Strictly vegetative plants having only a primary axis are monopodial.

The first leaf of the secondary axis is a closed, bladeless, sheathing bulb scale located inside the resistant layer and corresponding to S in Figure 1. Since this sheath is disrupted when growth is resumed in the spring, it is usually present only as fragments and frequently is not recognizable at all. The sheathing bulb coat (S, fig. 1), is the first leaf of the tertiary axis that will develop into next year's bulb.

The fleshy cataphylls (Fc and Fc') are the second leaves of the secondary and tertiary shoot axes respectively. They are typical tunicate bulb scales. The fleshy cataphyll of the present season (Fc') will constitute the bulk of next year's bulb and is a storage organ, chiefly of water. The fleshy cataphyll of last year (Fc) is distended, accommodating the new vegetative growth that is developing inside. This cataphyll remains firm until early March when it begins to disintegrate, the remaining nutrients presumably being translocated to the new growth.

The open end of the developing fleshy cataphyll (Fc') forms a tubular canal (Ca) that leads from the apex to the base of the cataphyll and is enlarged below around the shoot apex (A). As new leaves develop from

the shoot apex they extend up this canal until, in the following spring, Fc' becomes distended, resembling the fleshy cataphyll of the preceding year (Fc) as shown.

Two non-fleshy cataphylls (C1 and C2) are located inside the fleshy cataphyll. Below ground they resemble the bases of the foliage leaves (L1 and L2); above ground they are colorless sheathing membranes. If the above-ground portion of the plant had been included in Figure 1, C1 and C2 would be shown as closed, nested tubes, enclosing the tips of L1 and L2. As the growing season progresses the foliage leaves elongate rapidly, breaking through the tips of the cataphylls, and appear as concave-convex leaf blades with sheathing bases. The two cataphylls persist as sheathing membranes at the base of the foliage leaves.

The sheathing base of the inner leaf (L2) forms a cylindrical passageway, extending to a point above ground where the leaf sheath ends and the blade begins. The inflorescence (F) which terminates the shoot axis, grows up through this passageway from its point of origin along the union between the sheath (S) and the inner leaf base.

The sheath, as noted earlier, is the first leaf of an axillary branch that will develop into next year's bulb. It is a fairly thin cataphyll, snugly enclosing the fleshy cataphyll; its apical portion is thickened and conical and extends into the cylindrical passageway formed by L2.

The cataphylls (C1 and C2) and the outer leaf base (L1) show slight development of resistant thickening at their bases, but it is the inner epidermis of L2 that develops this thickening to the greatest extent, forming, eventually, the resistant layer, R. The sheath (S) shows the same modification on both the inner and outer surfaces.

During the winter months the epidermal cells that will form the resistant layer appear identical with other epidermal cells of the plant. About mid-March in Pullman the cells begin to increase in size in the plane of their short axis (e.g., perpendicular to the surface). As this increase in size continues strands appear across the short axis of some cells. These strands (presumably trabeculae) have a typical cellulose stain reaction (Mullen, 1928). By early April the cells have almost reached their mature size and each cell has cellulose thickenings, deposited in layers along the inside and lateral walls. In general the outer cell walls show no thickenings, though frequently a tuft-like mass of cellulose strands may appear on the inner surface (Mullen, 1928).

The mature condition, observed in late April or early May, is essentially that just described. There is only a slight increase in cell size. However, there is a distinctly different staining reaction. During April the thickened walls are impregnated with lignin; until this is complete the staining reaction is not uniform, varying with the amount of lignin present. When the impregnation is complete a deep red color results from staining with safranin or treatment with concentrated HCl and phloroglucin.

Members of the *Allium acuminatum* alliance are dormant during the hot dry months of summer and early fall. It has been demonstrated repeatedly, with pressed specimens, that the resistant layer is responsible for conserving moisture in the fleshy cataphyll during this period. Flowering plants collected and pressed during the spring have bulbs that will sprout the following year provided the resistant layer is not disrupted by the pressing. This is true even when the specimens are dried in a drying cabinet for up to three weeks. Numerous herbarium specimens of all species in the alliance show sprouts that were formed a year after the plants were pressed. In bulbs where the resistant layer is disrupted, the fleshy cataphyll dries out and no sprouting occurs the following year.

The resistant layer, while very conspicuous and highly developed, is not unique to the *Allium acuminatum* alliance. Treatment with concentrated HCl and phloroglucin indicates that the inner epidermis of the inner leaf base forms a sclerified resistant layer in *A. crenulatum*, *A. glandulosum*, and *A. tribracteatum* Torr., a non-rhizomatous member of the *A. falcifolium* alliance. The resistant layer in these species, however, is thin and does not show the prominent cellular reticulation found in the *A. acuminatum* alliance, but it serves the same protective function. This is easily observed in herbarium specimens, as these species also show the ability to sprout a year or more after being pressed and dried, provided they are not crushed in the process.

Bulbs, in the garden, root and sprout after the fall rains begin in early to mid-November. Bulbs of all species maintain their dormancy even when watered during the summer, though such plants may sprout two to three weeks ahead of those receiving no summer water. In an attempt to break the dormancy, dry, mature bulbs of several species were planted in sand and subjected to 4°C with once-a-week watering. This treatment was begun in late July, 1968 and continued for eight weeks, after which the bulbs were moved to the greenhouse and watered as needed. When these bulbs were compared with those grown continuously in the greenhouse where watering began in late November, the sprouts of the experimental group appeared above ground less than two weeks before those of the greenhouse specimens. The fact that bulbs receiving adequate summer moisture do not sprout earlier indicates that a very strong dormancy, which can be broken only after a fairly long rest period, prevails in these species.

Non-rhizomatous members of the *Allium acuminatum* alliance, as is common in bulbous monocotyledons, produce two types of bulbs each year. The first is the single bulb arising as an axillary bud from the inner leaf base; since this bulb serves to continue the plant that produced it, it is termed a renewal bulb (Mann, 1960). As the axis of the renewal bulb develops during the first spring, forming a sheath, fleshy cataphyll, and two non-fleshy cataphylls, one or more buds may appear

in the axils of each of the newly formed cataphylls. These buds will also develop into bulbs, and, as they serve for vegetative multiplication, they are termed increase bulbs (Mann, 1960).

If a small number (two to four) of increase bulbs are formed, they develop only in the axil of the inner cataphyll, but if a larger number are formed both cataphylls are usually involved. Development of the increase bulbs occurs simultaneously with the further development of the renewal bulb. If an increase bulb bud forms in the axil of the inner cataphyll, it will develop two foliage leaves, as does the renewal bulb. A bud developing in the axil of the outer cataphyll, however, would first produce a non-fleshy cataphyll, corresponding to the inner cataphyll of the renewal bulb, in addition to the two foliage leaves. In both cases the leaves of the increase bulbs are included within the sheath, fleshy cataphyll and one or both non-fleshy cataphylls of the renewal bulb. Subsequently, in the second spring, the inner leaf base of the renewal bulb and each increase bulb forms a resistant layer, inside of which a new sheath and fleshy cataphyll develop. In this manner both types of bulbs produce their own renewal bulbs for the following year. The actual positions of the renewal bulbs depend on whether or not the shoot axis involved produces an inflorescence. The original renewal bulb and, commonly, one or more of the increase bulbs will flower. Those bulbs producing an inflorescence form a renewal bulb in the axil of the inner leaf base, while those not flowering apparently produce the renewal bulb terminally on the shoot axis. Separation of the renewal bulbs occurs when the surrounding leaf tissues disintegrate, leaving each bulb invested by its own resistant layer. By this stage it is usually impossible to distinguish between the original renewal and increase bulbs as they are all approximately the same size.

Considerable difference exists in the *Allium acuminatum* alliance as to the number of increase bulbs formed in any one year. Under field conditions it was observed that vegetative multiplication may occur infrequently, with one or more years between the production of successive increase bulbs. For example, *A. davisiae* from the Mojave desert may have a single bulb invested by the resistant layers of ten or more growing seasons, indicating that no increase bulbs were formed during this period. At the other extreme, *A. hyalinum*, growing under moist soil conditions on the border of the San Joaquin Valley, may have as many as six increase bulbs produced in a single season. Generally, plants collected in the field tend to have one or two increase bulbs formed each year. Plants from the same populations, grown under more favorable soil and water conditions in the garden, have larger bulbs, increase annually, and, in *A. hyalinum* and *A. amplexans*, at least, may produce as many as eight to twelve increase bulbs per year.

In addition to differences in the rate of vegetative multiplication, the morphology of the non-rhizomatous species, or individuals within species,

may differ in detail from the general type described. Some individuals of *Allium acuminatum*, for example, have three cataphylls and three foliage leaves. This would add a C3 and L3 to Figure 1, but otherwise no difference is observed from the previous description; likewise *A. dichlamydeum* has two or three cataphylls and three to six leaves. Considerable variation is also observed in the size of mature bulbs; flowering size bulbs of *A. crispum*, *A. dichlamydeum*, and *A. praecox* are commonly 1–2 cm in diameter, while those of *A. hyalinum* and *A. hickmanii* seldom exceed 6 mm. The other species of the alliance fall between these extremes. Again, while these differences in detail exist, the general morphology is the same in all of the non-rhizomatous species.

The rhizomatous species, as represented by *Allium unifolium* (fig. 2), do not differ significantly from each other, regardless of the length of the rhizome, and, except for the rhizome (Rz) have the same general morphology as the non-rhizomatous species. The bulb at the end of the rhizome (Rz) in Figure 2 represents the stage observed in late spring prior to anthesis. This is a renewal bulb developing in the axil of the inner leaf base (L2). Here, as in the non-rhizomatous species, the in-

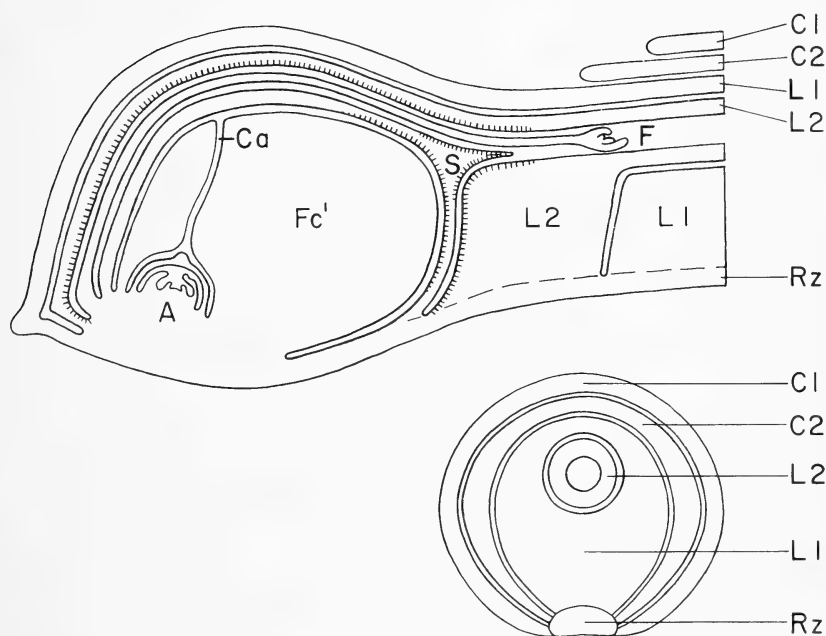


FIG. 2. Median-longitudinal section through a rhizome and new bulb and cross section of a rhizome of *Allium unifolium*: A, apical meristem; Ca, canal; S, sheath; F, scape (current year); Fc', new fleshy cataphyll; L1, L2, leaf bases; C1, C2, cataphyll bases; Rz, rhizome.

florescence (F) terminates the shoot axis and the sheath (S) and fleshy cataphyll (Fc') are the first leaves of the secondary axis. The fleshy cataphyll and resistant layer of the preceding year, corresponding to Fc and R in Figure 1, are not shown because the elongating rhizome leaves them behind. As the bulb continues to develop, two cataphylls are produced by the apical meristem (A) and grow into the tubular canal (Ca) formed by the open end of the fleshy cataphyll. Subsequently, the buds of one or two increase bulbs may develop in the axil of the inner cataphyll. During this period the plant flowers and the leaf and rhizome tissues outside the new resistant layer (indicated by shading) disintegrate. Like the non-rhizomatous species, the rhizomatous ones become dormant after flowering and maintain their dormancy during the warm, dry summer months.

In early spring of the following year roots develop below A (fig. 2) and shortly thereafter the cataphylls and leaves resume growth, breaking through the resistant layer above the canal. With the resumption of growth, one, two, or three rhizomes develop from near the shoot apex (one rhizome developing for the renewal bulb and each increase bulb formed the preceding year). These break through the resistant layer adjacent to the rootpad carrying with them the apical meristem and leaf and cataphyll bases, which form tubular extensions as they grow. Growth of the rhizome and the tubular extensions is presumed to be due to intercalary meristems. Cell division has not been observed and, because of the highly condensed nature of the shoot, the exact relationship between the apical meristem and the rhizome is unclear. However, the shoot apex is certainly carried along by the elongation, if not the division of cells below those that can properly be considered to be included in the apical meristem.

The old fleshy cataphyll and resistant layer are again left behind by the elongating rhizomes. As in the non-rhizomatous species the fleshy cataphyll disintegrates with its stored nutrients being, presumably, translocated to the new growth.

Shortly after the rhizome begins to grow the growth potential of the cataphylls is exhausted and, as they cease to elongate, the rhizome and leaf bases break through them. Thus, when the rhizome stops growing its tip is surrounded by the outer leaf base as all tissues outside it have been left behind.

Few roots develop along the rhizome, and the rootpad formed by the old bulb remains functional throughout the growing season. It is connected to the rhizome by vascular bundles.

The leaf and cataphyll bases differ from those of the non-rhizomatous species in being asymmetrical. The connection of the leaf base to the rhizome is elongate on the upper side of the rhizome (fig. 2). In addition to the asymmetrical connection, the leaf base, in this area, is thickened by the presence of substantial amounts of parenchyma, which is absent

in the rest of the leaf base. As with the fleshy cataphylls, this parenchyma tissue apparently acts in a storage capacity. Development of the renewal bulb of the following year's plant occurs during and immediately after the growth of the rhizome. Disintegration of the leaf tissues follows as the new fleshy cataphyll matures and this disintegration, presumably, contributes nutrients and/or water to the development. In the species with short rhizomes the elongate, fleshy portion of the leaf base is considerably reduced, reflecting the reduced length of the rhizome.

The scape (F) originates at a point along the union between the sheath and the inner leaf base, just as it did in the non-rhizomatous species. Generally the scape grows up the cylindrical passageway formed by the inner leaf base and through the canal in the preceding year's fleshy cataphyll, before it appears above ground. In *Allium unifolium*, however, due to the length of the rhizome, the scape frequently breaks out of the leaf bases below the old fleshy cataphyll, appearing above ground at some distance from the leaves. In field collections of this species only one scape is produced, regardless of the number of rhizomes formed by a single bulb. Further it was determined that the original renewal bulb produces the scape while the increase bulbs, carried on separate rhizomes, produce only somewhat depauperate leaves. Populations grown in the garden at Stockton often develop two or three scapes, but even here the scape associated with the renewal bulb predominates in size and the others are significantly smaller.

The length of the rhizome is one of the most distinctive features separating rhizomatous species of the *Allium acuminatum* alliance. In addition, the species with short rhizomes, including *A. crenulatum* of the *A. falcifolium* alliance, tend to have only two or very rarely three leaves; *A. unifolium*, on the other hand, may have up to six. The bulbs of all species except *A. mirabile* are ovate, but there is considerable variation in size. In *A. unifolium* the bulbs are 1.0–1.5 cm in diameter, while in *A. bolanderi* and *A. dictyon* they are less than 1 cm in diameter. In *A. crenulatum* the bulbs are larger, 1–2 cm in diameter, but it should be noted that several of the species in the *A. falcifolium* alliance have bulbs that are larger than those of any of the species in the *A. acuminatum* alliance. In *A. mirabile* the bulbs are elongate-ovate and very irregular in shape, superficially resembling small tubers. The long axis of these bulbs rarely exceeds 1 cm. In spite of these differences in detail the rhizomatous species, like the non-rhizomatous ones, have a remarkable similarity in their bulb morphology.

The bulbs of *Allium glandulosum*, the second species with long rhizomes, superficially resemble those of *A. unifolium*, but considerable divergence in morphology between the two species is observed. *Allium glandulosum* flowers from mid-summer to fall rather than in the spring and, as a result its seasonal development is at least three months later than any of the other species investigated. The developmental sequence,

except for the time lag, is similar to *A. unifolium*; there are, however, some rather important differences in the rhizome. The meristem of the renewal bulb is not passed to a rhizome, but rather it develops within the confines of the current year's leaf bases in the manner of the non-rhizomatous species investigated. Thus the continuity of the main bulb is maintained. The rhizomes carry the apical meristems of the increase bulbs. Furthermore, the apical meristem of the increase bulb produces a succession of asymmetrical fleshy cataphylls beyond the attachment of the leaf bases, each succeeding cataphyll breaking through the base of the previous one as the rhizome elongates. The rhizome in *A. glandulosum* is 8–12 cm long and may branch as secondary increase bulbs form from buds in the axils of one or more of the succession of fleshy cataphylls. As with *A. unifolium*, new increase bulbs are borne terminally on the rhizome, or its branches, but in their development they have left behind any direct association with the bases of foliage leaves or the passageway through which the leaves and scape emerge. It is as if the apical meristem (A in fig. 2) continues to produce successive fleshy cataphylls, only the final one or ones of which enter into the formation of the mature increase bulb.

Normally a single scape is formed by *Allium glandulosum* and it is associated with the main bulb. Just as in the other species, the scape is terminal on the shoot axis and is located along the union between the inner leaf base of the current bulb and the sheath, which represents the first leaf of the axillary renewal bulb. Additional scapes associated with increase bulbs are rarely produced. They arise terminally on the axis of the increase bulb in a position corresponding to the scapes in *A. unifolium* (fig. 2). The additional fleshy cataphylls in *A. glandulosum* mean that the scape is more remote from the bulb formed at the tip of the rhizome, but otherwise no difference is observed from the position of the scape in *A. unifolium*.

DISCUSSION AND CONCLUSIONS

Judged by the organization of their bulbs, the non-rhizomatous species of the *Allium acuminatum* alliance form a closely related and natural group. As noted earlier, all of the plant organs in the non-rhizomatous species are found in the same sequence in the rhizomatous ones. Furthermore, these structures are in the same relative positions, except that the rhizome carries the leaf and cataphyll bases, and all of the parts inside these organs, outside the confines of the preceding year's fleshy cataphyll and resistant layer. In the non-rhizomatous species, on the other hand, all growth occurs within the confines of the old fleshy cataphyll and resistant layer. Except for the rhizome, the general development and morphology of the bulb are identical in both groups.

In comparing the morphology of members of the *Allium acuminatum* alliance with that reported by Mann (1960) for the European section

Molium, a number of similarities as well as striking differences are noted. The first leaves of a main or renewal bulb in sect. *Molium*, corresponding in position to the sheath in *A. acuminatum*, are a pair of bladeless leaf bases that become fused along their adjacent epidermal layers. Because the inner epidermis of the outer of these two leaves becomes sclerified, Mann termed them protective leaves. Functionally the protective leaves correspond to the resistant layer in the *A. acuminatum* alliance, but the derivation of the two structures is dissimilar. The resistant layer of the *A. acuminatum* alliance develops from the inner leaf base of the mother bulb, or primary axis, while the protective leaves of sect. *Molium* develop as the first leaves of the renewal bulb, or secondary axis. As a result, the remains of the scape are included within the resistant layer in the former and outside the protective leaves in the latter.

The protective leaves of the increase bulbs in sect. *Molium* are surrounded by a second type of bladeless leaf, absent in the renewal bulb, which Mann called a prophyll. If, in fact, the protective leaves correspond to the sheath in the *Allium acuminatum* alliance, then there is no organ corresponding to the prophyll. This interpretation is supported by the presence of a sheath in both the renewal and increase bulbs of the *A. acuminatum* alliance and the presence of protective leaves around both types of bulbs in sect. *Molium*. The *A. acuminatum* alliance has no type of leaf that is present in the increase bulbs, but lacking in the renewal bulb, thus corresponding to the prophyll in sect. *Molium*.

The protective leaves in sect. *Molium* surround a food storage leaf that corresponds in structure and function to the fleshy cataphyll of the *Allium acuminatum* alliance. Inside the food storage leaf is a single bladeless sprout leaf that corresponds to the cataphylls in Figure 1. Mann reported only a single sprout leaf in each bulb of sect. *Molium* while, as pointed out earlier, two or three cataphylls occur in each bulb of the *A. acuminatum* alliance.

The bases of the foliage leaves are similar in both groups, though the bulbs of sect. *Molium* tend to have a larger number of leaves per bulb. Above ground, the leaf blades of sect. *Molium* are larger and more prominent.

Branching of the shoot axis is more prolific in sect. *Molium*. In addition to the branches terminated by increase bulbs, there are from one to five branches terminated by inflorescences and one terminated by a renewal bulb. In the *Allium acuminatum* alliance, on the other hand, only two branches are found in addition to those bearing increase bulbs, one terminated by an inflorescence and the other by a renewal bulb.

The development of increase bulbs is similar in both groups, but the position and developmental sequence are different. In sect. *Molium* the new renewal bulb is differentiated in the axil of the upper foliage leaf in early autumn. Following the formation of this renewal bulb, the increase

bulbs develop in the axils of the foliage leaves immediately below it. Generally these increase bulbs do not develop leaves in the spring after they are differentiated, but rather develop their first foliage leaves in the following spring, some eighteen months later. Only under the most favorable garden conditions were leaves and inflorescences formed in the first year. The increase bulbs varied greatly in size, but were usually very much smaller than the renewal bulbs.

In the *Allium acuminatum* alliance the increase bulbs develop concurrently with the main bulb axis and prior to the differentiation of a new renewal bulb. The increase bulbs develop in the axils of the cataphylls and invariably produce green foliage leaves and, commonly, inflorescences in the spring following their initiation. Because of the simultaneous development of the increase bulbs and the main bulb, and the early development of foliage leaves, the increase bulbs are approximately the same size as the renewal bulb at the end of their first growing season. In both groups the separation of the renewal and increase bulbs occurs when the surrounding leaf tissues disintegrate.

Mann concluded from his investigation that the species in sect. *Molium* form a closely related natural group. Members of the *Allium acuminatum* alliance also are closely related. The general bulb morphology of these two groups, as would be expected, is similar. Bulbs of both groups are composed of several distinct types of leaves without intergrading forms. They are ecologically specialized for maturation in the spring and long periods of summer dormancy. Along the same line, the enclosure of each bulb by a firm sclerotic layer has been demonstrated to be of ecological significance in enabling the bulbs to resist desiccation during dormancy.

The differences in these two groups, however, particularly in the origin of the resistant layer, the order of development of the increase and renewal bulbs and the lack of a prophyll, indicate that members of the *Allium acuminatum* alliance have in common a number of important characters that separate them from sect. *Molium*. The fact that *A. crenulatum* and *A. glandulosum* have an organization and developmental sequence similar to the rhizomatous species of the *A. acuminatum* alliance indicates further that the three alliances involved are also closely related. If, as seems probable, the non-rhizomatous species of the *A. falcifolium* and *A. kunthii* alliances have an organization similar to the non-rhizomatous members of the *A. acuminatum* alliance, this will be further evidence of a close relationship among the New World species of *Allium*.

SUMMARY

Bulb organization and seasonal development are described for the rhizomatous and non-rhizomatous species of the *Allium acuminatum* alliance and for the rhizomatous species *A. crenulatum* of the *A. falcifolium*

folium alliance and *A. glandulosum* of the *A. kunthii* alliance. The two types have a highly similar morphology except for the rhizome. Except for *A. glandulosum*, the species begin growth in the late fall or winter, flower from February to June and are dormant throughout the summer. *Allium glandulosum* blooms in the summer and fall and there is a corresponding time lag in its development. Four distinct types of leaves make up the bulb including: a sheath, a fleshy storage cataphyll, bladeless leaf sheaths or cataphylls, and foliage leaves. Sclerification of the inner epidermis of the inner leaf base forms a heavy, cellular-reticulate, resistant layer in the *A. acuminatum* alliance. The resistant layer effectively prevents desiccation of the bulb. The shoot axis annually produces two kinds of bulbs: a renewal bulb differentiates in the the axis of the upper foliage leaf, serving to continue the plant, and one or more increase bulbs may differentiate in the axils of the cataphylls, serving for vegetative multiplication. Bulb size appears to be one factor that triggers the differentiation of increase bulbs and determines how many will develop. In comparing bulb morphology of the species investigated with the bulbs of the European sect. *Molium*, it was found that they differed in the origin of the resistant layer, the development of increase bulbs, and the absence of a fifth type of leaf, the prophyll, present in sect. *Molium*.

TABLE 1. SOURCES OF MATERIALS USED IN THE INVESTIGATION OF BULB MORPHOLOGY IN WESTERN AMERICAN ALLIUMS. (Vouchers have been deposited at CPH and WS.)

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- A. acuminatum*. Wash., Whitman Co., 2 mi. N of Almota, *McNeal* 377. Calif., Trinity Co., 2.8 mi. E of Forest Glen, Rattlesnake Creek, *McNeal* 504.
- A. amplexens*. Calif., Del Norte Co., 9.4 mi. N of Gasquet, *McNeal* 412; Mariposa Co., 2.1 mi. N of Merced River on Rte 49, *McNeal* 490.
- A. bolanderi*. Calif., Shasta Co., 1.1 mi. S of Round Mt., *McNeal* 399.
- A. crispum*. Calif., San Benito Co., Rte. 25, 4.1 mi. S of Tres Pinos, *McNeal* 495.
- A. davisiae*. Calif., Kern Co., Rte. 14, 3 mi. S of Mojave, *Ownbey* 3502.
- A. dichlamydeum*. Calif., Sonoma Co., Rte. 1, 3 mi. N. of Bodega Bay, *McNeal* 411.
- A. dictuon*. Wash., Columbia Co., Blue Mts., 0.5 mi. N of Weller Butte, *McNeal et al.* 415.
- A. hickmanii*. Calif., Monterey Co., Monterey, Veterans Memorial Park, *McNeal* 484.
- A. hyalinum*. Calif., Stanislaus Co., Rte 132, 1.5 mi. W of La Grange, *McNeal* 393.
- A. lacunosum* var. *lacunosum*. Calif., Marin Co., Tiburon Peninsula, *McNeal* 500.
- A. lacunosum* var. *micranthum*. Calif., San Benito Co., above entrance station, E side Pinnacles National Monument, *McNeal* 496.
- A. mirabile*. Calif., Siskiyou Co., 2.6 mi. W of Hilt, *Ownbey and Mingrone* 3490.
- A. peninsulare*. Calif., Kern Co., Rte. 178, 1.5 mi. E of Onyx, *McNeal* 389; San Mateo Co., Jasper Ridge, Stanford University, *Raven s.n.* in 1968.
- A. praecox*. Calif., San Diego Co., 3.5 mi. E of Chula Vista, *McNeal* 390.
- A. serratum*. Calif., Stanislaus Co., Del Puerto Canyon, *McNeal* 395.
- A. unifolium*. Calif., San Luis Obispo Co., Santa Barbara Rd., Atascadero, *Hardham* 5502.
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NOTES AND NEWS

IMPATIENS PARVIFLORA IN BRITISH COLUMBIA.—*Impatiens parviflora* DC., a native plant of Central Asia, has become established in Europe and eastern Canada. It has not, however, been reported from western North America, although it has now been collected from two places in southwestern British Columbia. Moreover, the population at one of these locations has maintained itself for at least twenty years. The first collection was made in 1949 (*J. W. Eastham* 16,477, UBC). Eastham found a small plant growing in sandy soil between the beach and the road at Spanish Banks, a popular beach on the north side of Point Grey peninsula, Vancouver, B.C. He noted on the herbarium sheet that there were several, more robust, plants growing in the wooded area on the opposite side of the road. When this area was revisited in 1972, the species was well established in the woods, but no plants were found on the beach side of the road (*Barkworth* 527, WS).

In 1972, I found this species at Lions' Bay, 8 miles north of Horseshoe Bay, West Vancouver, approximately 15 miles due north of Spanish Banks (*Barkworth* 513, 523, WS). Here, too, the plants were growing beside a road, highway 99, and near a developed area, Lions' Bay community. The road has been cut into the hillside, creating a steep gravel bank on the east side. Several plants of *Impatiens parviflora* were growing on a small gravel pile located at the foot of this bank. They were more abundant on the east side of the gravel pile where they received some degree of protection. Apart from this topographic protection the area is very open. In addition the road bank is not very stable. Fifty feet from the *I. parviflora* population there were frequent small falls of gravel, even on a dry summer day. The highway department presents yet another hazard. Several sections of the road are being improved at the present time, so the site may be destroyed by highway work crews. It appears, therefore, that the success of the species in this area will depend, in large part, on its becoming established in a 'safer' location before the present site is destroyed.—MARY E. BARKWORTH, Department of Botany, Washington State University, Pullman 99163.

A NEW SUBSPECIES OF LUPINUS BURKEI

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Several years ago a lupine collected by Arthur Kruckeberg (2485—MONT), from the Blue Mountains of Oregon was received on a loan. This specimen differs from any taxon in *Lupinus* known from the western United States, and we viewed it as a new taxon or possibly of hybrid origin. For three years we unsuccessfully sought this lupine in the field, and finally located it in 1971.

Although the area was still under snow in late June, and the plants had a radical cluster of leaves with a solitary subscapose flowering culm by late July, fruits were developed by mid-August. For perennial lupines to develop mature legumes from early anthesis in three weeks is very rapid.

The population extends continuously about a mile to one and a half miles along Oregon State Highway 204 near the highest point between Langdon Lake and Elgin, Union Co. The lupine appears to have a restricted, isolated niche at this high point in the heart of the Blue Mountains, an area that has a dense forest of mature spruce, larch, and lodgepole pines that holds the snow longer than open areas.

Extensive morphological study of this lupine indicated similarities with several other taxa and suggested relationship either with the *Lupinus latifolius* complex or the *Lupinus polyphyllus* complex. The Oregon plants (fig. 1) are most closely related to *L. burkei* (of the *L. polyphyllus* complex), but differ from other populations of this species in various morphological details (Table I). *Lupinus burkei* subsp. *burkei* and *L. polyphyllus* are illustrated elsewhere (Dunn & Gillett, 1966). Due to the morphological, biochemical, and ecological distinctiveness, relative geographical isolation, and well established nature of this Oregon Blue Mountain lupine, we have discarded immediate hybrid origin as an explanation for its origin and describe it herein as *Lupinus burkei* subsp. *caeruleomontanus*.

Since seed alkaloids have proven beneficial in comparing perennial lupine affinities (Cox, 1972), comparisons of *Lupinus burkei* ssp. *burkei* and *caeruleomontanus*, *L. polyphyllus*, and *L. latifolius* were made employing the methods of extraction and plating described by Cox (1972).

The TLC (silica gel—G) solvent system that proved most successful in separating the greater number of alkaloids was adapted from Cho & Martin (1971) and consisted of chloroform/methanol/ammonia (95:4:1). Average R_f values were calculated by analyzing six to ten populations of each taxon, with the exception of *caeruleomontanus*, of which only two samples were available from populations separated by approximately

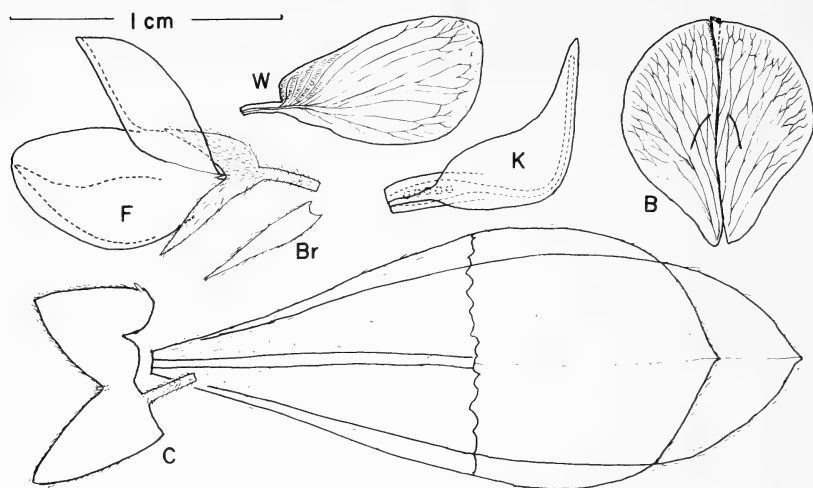


FIG. 1. Floral parts and a typical leaflet of *Lupinus burkei* subsp. *caeruleomontanus*. The flower viewed from the left side—F, banner—B, wing—W, keel—K, calyx, cut along the left lateral sinus, unfolded and the inside view shown—C, and a bract—Br, are illustrated. All parts are drawn to the typical conformation of the structure with the size the mean value of the measurements of fully developed flowers with one measurement from each of 25 plants from population samples of two locations. Leaflets drawn to one-third the scale shown for the floral parts.

one mile. Several plants from each population were also analyzed to test the intrapopulational variation of the alkaloids. Reference compounds of lupanine, sparteine, 13-hydroxylupanine and 17-oxolupanine were gifts of Professors Y. D. Cho and R. O. Martin, University of Saskatchewan. Alkaloids were visualized and identified by spraying with both Dragendorff and iodoplatinate reagents.

The alkaloids of *caeruleomontanus* are more similar to those of *L. burkei* subsp. *burkei* than to other taxa examined (Table 2).

***Lupinus burkei* Wats. subsp. *caeruleomontanus* Dunn & Cox, subsp. nova.**

Holotype: Oregon; Union Co., Near divide, between Langdon Lake and Elgin, south of Woodland Campground, northwest-facing roadcut, Aug. 19, 1971, *Dunn 18278* (UMO). Isotypes will be distributed to: CAS, DS, F, GH, K, MO, NY, ORE, OSC, RM, RSA, UC, US, WIS, WS, & WTU. Paratypes: *Dunn 18276* (same herbaria as 18278); *Kruckeberg 2485* (MONT).

Plantae perennes, 2–3 dm altae sub anthesi, 4–5 dm sub fructu; caulibus gracilibus, cavis, 2–3 mm diametro, span-strigulosi, unifolius in caule sub anthesi racemi primarii; foliis multis radicalibus; petiolis ad 15 cm longis; foliolis 6–7, obovatis, supra glabris, maximis 4.5–6.0

TABLE 1. DIAGNOSTIC MORPHOLOGICAL TRAITS OF THE SUBSPECIES OF LUPINUS BURKEI AND SIMILAR TAXA.

Diagnostic Traits	Taxa			
	<i>L. burkei</i> ssp. <i>caeruleomontanus</i>	<i>L. burkei</i> ssp. <i>burkei</i>	<i>L. polyphyllus</i>	<i>L. latifolius</i>
Plant height (dm)	2-3	4.5-9.0	5-15	3-12
Cauline nodes	1-3	3-4	3-5	over 6
Leaflet No.	6-7	7-11	10-17	7-9
Leaflet length (cm)				
(largest)	4.5-6.0	4-10	7-15	4-10
Petiole length (cm)				
(longest)	10-14	15-30	14-62	3-10
Flower length (mm)	8-10	12-14	12-14	10-14
Bracts	caducous	generally persistent	caducous	caducous
Bract length (mm)	4-6	10-15	10-13	8-12
Pedicel length (mm)	2	2-4	5-15	6-12
Keel	glabrous	glabrous or ciliate at midpoint	glabrous	ciliate near claws
Pod length (cm)	1.5-1.8	2-3	2.5-5.0	3
Seed No.	4-6	6-8	6-10	7-10

TABLE 2. DISTRIBUTION OF ALKALOIDS AMONG LUPINUS TAXA

A. R_f values and relative amounts observed (t = trace, + = small, ++++ = copious). Unidentified alkaloids are numbered.				
Taxa				
Alkaloid	R_f	<i>L. burkei</i> ssp. <i>caeruleomontanus</i>	<i>L. burkei</i> ssp. <i>burkei</i>	<i>L. polyphyllus</i> <i>L. latifolius</i>
1	.00	t	t	t
2	.01	t	t	t
Sparteine	.08		+	
4	.12	+	++	
13-Hydroxy-lupanine	.21		++	
6	.23	t	t	
7	.33	+	+	
Angustifoline	.46		+	
9	.49	t	t	
10	.57	++	++	+
Lupanine	.70	++	++	+++
12	.79	++	++	++++
B. Percent similarity of alkaloids of these taxa.				
Taxa	<i>caeruleomontanus</i>	<i>burkei</i>	<i>polyphyllus</i>	<i>latifolius</i>
<i>caeruleomontanus</i>	100			
<i>burkei</i>	75	100		
<i>polyphyllus</i>	44	33	100	
<i>latifolius</i>	22	17	20	100

cm longis, 15–22 mm latis; pedunculis 7–10 cm longis; racemi verticillati ad subverticillatos; bracteis 4–6 mm longis, caducis; pedicellis 2–3 mm longis; calycibus bilabiatis, labiis ambobus integris generaliter, bracteolis in sinis lateralibus 0.1–0.7 mm longis; floribus subviolaceis ad subazulinos praeter apicem carinae atropurpureum; vexillo obovato, 7.6–9.2 mm longo, 6.0–8.4 mm lato, reflexo prope in medium; carina glabra, angula 90–112°; leguminibus 15–18 mm longis, 5.0–5.5 mm latis; seminibus 4–6, 4 mm longis, 3 mm latis.

Plants perennial, 2–3 dm tall at anthesis, elongating to 4–5 dm by fruiting; stems slender, hollow, 2–3 mm dia., sparsely strigulose, one cauline leaf at anthesis of the primary raceme, 2–3 by fruiting; multiple radical leaves with petioles to 15 cm long; stipules of cauline leaves 2.0–4.5 mm long, connate to petioles 1–2 mm; leaflets 6–7, obovate to broadly oblanceolate, tip mucronate, glabrous above, very sparsely strigulose below, largest 4.5–6.0 cm long, 15–22 mm wide; peduncles 7–10 cm long; racemes verticillate to subverticillate, internodes 6–11 mm distant; bracts lance-attenuate, 4–6 mm long, caducous; pedicels 2 mm long at anthesis, 2.5–3.0 mm in fruit, sparsely spreading pilose hairs 0.2–0.3 mm long; calyx sparsely pilose without, glabrous within, the lips commonly both entire, or the upper lip with a notch 0.1–0.8 mm deep, the lower-lip 3.8–5.6 mm long, upper-lip 3.4–5.2 mm long, bracteoles at lateral sinuses 0.1–0.7 mm long, attached near the sinus lip, lips connate laterally 1.2–2.0 mm; corolla glabrous, pale lavender-blue, except the keel-tip deep purple; banner obovate, 7.6–9.2 mm long, 6–8.4 mm wide, reflexed 3.6–4.6 mm, appressed 3.8–5.4 mm, reflexed/appressed ratio 0.8–1.0 (av. 0.87), the angle 117–133°; wings 8.0–10.2 mm long, 3.8–5.1 mm wide, the claws 1.4–1.8 mm long; keel 2.6–3.0 mm wide at midpoint, the tip slender, deep purple, the rest white, the angle 90–112°; pods 5.0–5.5 mm wide, 15–18 mm long, with pilose hairs 1–2 mm long; ovules 4–6; mature seeds 4 mm long, 3 mm wide, finely mottled dark brown on cream colored background.

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NOTES AND NEWS

A NEW GRASS FOR CALIFORNIA.—*Heleochloa alopecuroides* (Pill. & Mitterp.) Host. was found in Del Norte County, California, about 1 mile north of the Humboldt County line, approximately 8 miles inland and east of Highway 101, growing in scattered patches with other low herbs in moist silty sand along the strand of the Klamath River (C. E. Etienne s.n., 4 Sept. 1972, CAS and Dept. of Agriculture, Sacramento). It has not been reported from California according to Munz & Keck (A California Flora, 1959, and its Supplement, 1968) and to Hitchcock (Manual of the Grasses of the United States, rev. 1950). Its presumed point of introduction is Portland, Oregon, and it has been noted, for example, in eastern Washington along the Columbia River (Raven, Leaf. West. Bot. 8:200, 1957), commonly along the Willamette River near Corvallis, Oregon, (Chambers & Dennis, Madroño 17:92, 1963), along the Rogue River near Agness, Oregon (Baker, Madroño 17:197, 1964). However, it was not reported by Hitchcock et al. (Vascular Plants of the Pacific Northwest, 1969).—C. E. ETIENNE, Botany Department, California Academy of Sciences, San Francisco 94118.

ON THE GROWTH RATE OF A JOSHUA TREE.—The accumulated height of an unbranched Joshua tree (*Yucca brevifolia*) was 137 cm in November 1960, 150 cm in October 1962, 183 cm in October 1965, and 246.5 cm in May 1972. A terminal inflorescence was formed early in 1972. The growth increments therefore were 13 cm in 2 years, 33 cm in 3 years and 63.5 cm in 6 years for a total of 109.5 cm in 11 years. The tree under observation is located at Rose Mine in the San Bernardino Mountains of Southern California at an elevation of approximately 6800 feet (2100 meters) above sea level. The vegetation is a woodland dominated by *Artemisia tridentata*, *Juniperus osteosperma*, *Pinus monophylla*, and *Cercocarpus ledifolius*. The arborescent character of the associated vegetation suggests a more mesic environment than is usual for Joshua trees and therefore the observed growth rate of approximately 10 cm per year may be somewhat higher than average for this species. The leaves marked in 1960, as well as many of those situated lower on the stem, were green and apparently healthy and functional in 1972. An individual leaf, therefore, functions for more than a dozen years, perhaps for 15 to 20 years.—FRANK C. VASEK, Department of Biology, University of California, Riverside 92502.

CYTISUS MONSPESSULANUS L., ESTABLISHED IN SOUTHERN CALIFORNIA.—Previously, *Cytisus monspessulanus* has been reported as "perniciously" naturalized in California near the coast from Ventura County northward (Munz, P. A., A California Flora, 1959). Recently, I discovered a population of 256 living and 62 dead individuals of this species well established in oak woodland at the east end of William Hiesey County Park in the Cuyamaca Mountains, San Diego County (Keeley 2583, CSUSD).—JON E. KEELEY, Department of Biology, California State University, San Diego 92115.

CONRAD V. MORTON, 1905–1972.—Conrad V. Morton, a native Californian and senior botanist at the Smithsonian Institution, died July 29, 1972, in Washington, D.C., at the age of 67. Morton was born in Fresno and received his bachelor's degree from the University of California, Berkeley, where he was closely associated with W. L. Jepson. Mr. Morton joined the Smithsonian staff in 1928 and in 1948 became curator of the Division of Ferns, a position that he held at the time of his death. Perhaps best known for his studies of ferns and fern allies, Morton was also an authority on the Solanaceae and Gesneriaceae, and had a remarkably wide knowledge of vascular plants in general. Though he spent most of his professional life on the East coast, Morton maintained close ties with the botanical community on the Pacific coast. In memory of Mr. Morton, the staff and associates of the Department of Botany at the Smithsonian Institution have presented a cash gift to the California Botanical Society.

REVIEWS

The Biology and Chemistry of the Umbelliferae. By V. H. HEYWOOD, Ed. x +438 pp., illustrated. Supplement 1 to the Botanical Journal of the Linnean Society, Volume 64. Published for the Linnean Society of London by Academic Press, England. 1971. \$20.40.

EVERYTHING YOU EVER WANTED TO KNOW ABOUT THE UMBELLIFERAE? Twenty-two papers, presented as part of an international symposium on the Biology and Chemistry of the Umbelliferae held at the University of Reading, England in 1970, make up the text of this volume. Most of the contributors (6) are from the U.S.A. (Bell, Constance, Fairbrothers, French, Mathias, and Theobald) but in spite of this slant, there is good representation from Europe (Germany 3, France 3, England 3, among others) and one contributor each from Costa Rica and New Zealand. All of the papers are in English except, unfortunately, the several apparently excellent presentations from French workers. It would have been better judgement to publish *all* the texts in English, which is rapidly becoming the international language for Science. Certainly if all the contributors had made their presentations and published in their native language there would have been little intercommunication and much overlap, both at the symposium and in the text itself.

Constance sets the low key approach to the subject by his observation that even "... after three and a quarter centuries of successive and multinational effort, considerable disagreement still exists as to the proper delimitation of the family and even more uncertainty prevails as to its natural subdivisions and the criteria on which they should be erected". Even Heywood is humble reckoning as how his (and Dakshini's) scanning electron microscope "... study of the mericarps of *Caucalidae* is far from complete". And Moore (also from Reading) follows suit, stating (about chromosome studies), "—umbelliferous cytotaxonomy is still at the 'alpha' level". And Harborne (Reading too!) allows that "... our knowledge of the distribution and structure of these constituents [flavonoids] is still very superficial at the family level". And, further, "It is also too early to claim that knowledge of the flavonoids has contributed significantly to taxonomic revisions."

Only Hegnauer (except perhaps somewhere among those damnable papers in French), using chemical data, speaks with conviction suggesting, "Umbellales are not a climax group but may represent the stock from which *Asterales* evolved." A view also espoused by Bohlmann, using acetylenic compounds as taxonomic criteria.

In summary: It is evident on reading these papers that despite all this impressive body of research on the Umbelliferae, a vast amount of new information and reappraisal is needed before a systematic account of the family can be attempted. At least this reviewer can say that a hopeful beginning has been made. (Lest the reader think this summary somewhat unenthusiastic I wish to remark that, except for the words, "this reviewer", it is taken in full as the second from last paragraph of Heywood's introduction to this volume.)—B. L. TURNER, Department of Botany, University of Texas, Austin 78712.

The Agave Family in Sonora. By HOWARD SCOTT GENTRY. ii + 195 pp., 20 pages line drawings, 76 half-tones (often 2 or 3 per figure page), 7 maps and charts, 1 table 7 pages long. Agriculture Handbook No. 399. U.S. Government Printing Office, Washington, D.C. Available in paper from Superintendent of Documents, \$1.25 per copy.

This handbook is a valuable addition to the literature on *Agave*, with further coverage of other genera placed in this family as delimited by Hutchinson. It is based on many years of observations on populations of most of the 43 species and 2 subspecies known to occur in Sonora. The first 37 pages are devoted to the author's general observations, to his philosophical speculations applicable to the Agavaceae, to his interpretation of several historical developments in the taxonomy of the family, and to the utilization of the plants by natives and by Europeans.

The systematic arrangement follows that of J. Hutchinson (the Families of Flowering Plants. I. Ed. 2. 662-665, 1959), so includes *Manfreda*, *Polianthes*, *Yucca*, *Hesperaloe*, *Dasyllirion*, and *Nolina* in addition to *Agave*. Artificial keys are provided to the genera of the Agavaceae of Sonora, and at the beginning of the treatment of each of those genera to the species known to grow naturally in Sonora (when more than one such representative is known). Each species recognized is described rather fully (except for those whose flowers or fruits are unknown, and in such cases this lack is clearly indicated). The author compares related species, gives a statement of range of distribution as presently known, and adds critical notes about uses, habitats, associated plants, relationships with local animals, etc. He cites specimens examined and laments the inadequacy of the samples available in herbaria. They are inadequate both in number of collections and in the quality of many of the specimens on deposit. He attributes the failure of field botanists to collect larger numbers of specimens and to properly prepare them for herbarium storage, to their reluctance to spend sufficient time to split and scrape leaves, give frequent attention to drying processes, and their hesitancy about tackling the formidable spines of most *Agave* species. Another factor is the irregularity in the flowering periods of the Agaves in particular and to a lesser extent in the other genera, to secure which one often has to make several excursions into remote areas.

A list of the collections of *Agave* in herbaria (and seen by him) begins with those taken by Arthur Schott, who collected 2 numbers in 1855, and ends with 5 collected by Barclay and Arguelles in 1966. The total (representing those examined in herbaria by Gentry) comes to 223 numbers, 110 of these being those collected by Gentry, 40 by Gentry and Arguelles, and 5 by Gentry and Barclay! The other 66 collections were made by 12 different individuals or teams of field workers. This probably indicates the comparative attention devoted to *Agave* by Gentry and by other botanical explorers.

In addition to studying *Agave* in the field, the author cultivated many plants at his ranch near Murietta, California, and observed those grown for ornamental and study purposes in several botanical gardens.

The half-tone illustrations are of high quality and the pen and ink line drawings very good. The Handbook is printed on glazed paper, so reproduction of all illustrations is excellent. Typography is clear and errors are very few (the reviewer found none)!

The author describes 10 new species, 2 new subspecies, and reduces one of Jacobi's species to varietal rank. Literature cited includes 60 references and covers the field thoroughly. The book ends with a glossary just over 3 pages long and an inclusive index in which boldface numerals indicate the page on which the description of the taxon begins.

The Handbook will be useful to anyone with even a moderate interest in representatives of the Agavaceae, even though it deals with only those taxa known to grow in the state of Sonora, for the work is considered by its author to be a preliminary publication that he hopes to broaden into a monographic report on *Agave* in its entirety. This book more or less sets guidelines for the more extensive projected monograph.—IRA L. WIGGINS, Department of Biological Sciences, Stanford University, Stanford, California 94305.

A Computer-mapped Flora—A Study of the County of Warwickshire. By D. A. CADBURY, J. G. HAWKES, and R. C. READETT. 768 pp.. Academic Press. 1971. \$31.50

This publication, a heavyweight champion of nearly 6½ pounds, is one of the latest, and certainly the largest scion, of the old and honourable family line of British County Floras. It tends to leave a prospective reviewer gasping for words, like an architect suddenly confronted with a request for a critique of the great pyramid. The County Flora tradition represents a practical expression of the long and highly profitable co-operation between amateur and professional botanists in Britain, of which the Botanical Society *Atlas of the British Flora* is the most notable product to date. The present work, which includes flowering plants, ferns, and bryophytes, is the result of co-operation between the Birmingham Natural History Society and the Department of Botany of the University of Birmingham. Having started work along fairly traditional lines, the organizing committee introduced some radical changes in 1953. Recording was concentrated on a randomly selected 1 km square from each "tetrad" of 2 × 2 km squares of the British national grid, which fell within the boundaries of Warwickshire. The data collected were then put on to punched tape for later sorting and retrieval followed by automated map plotting. In a review primarily intended for consumption abroad, it is inappropriate to dwell on the finer details of the publication. Suffice it to say that it contains in good measure all the usual introductory ingredients. No less a figure than William Shakespeare himself is called upon to give testimony among the early records of the plants of his native county.

The real interest for readers outside Britain lies in the use of the computer for data handling and the incremental plotter for the production of the numerous distribution maps. The relatively simple maps of the BSBI *Atlas* had at most three symbols. Here we are confronted with no less than nine symbols representing nine major habitats. Thus if a species occurs in one locality in woodland a vertical line is printed, while if in another water is preferred, a W is shown on the map. Since, of course, many species occur in several habitats within a limited area, the result is a multiple superposition of symbols for many squares. The situation is further complicated as each symbol can occur in a light form (rare to occasional) and a heavy form (frequent to abundant), thus involving a total of 18 possibilities. Keys to the symbols are provided with each map, but are open to criticism in that they are printed at a different scale to the maps themselves, thus making the long and short vertical and horizontal lines potentially subject to confusion. A useful range of overlays is provided and through these, distributions can be compared with the patterns shown by topographical and physical features. While the reviewer has unstinted admiration for the conception and ingenuity of the scheme, he has grave reservation about the utility of the graphical presentation. The maps are so replete with information, that it is very difficult to interpret them in the manner intended and the reader is presented with a real problem in visual coordination. A second series of much simpler maps generated by a line printer, illustrates the distribution of 58 of the rarer flowering-plants and 184 of the more frequent bryophytes.

The Birmingham group has produced a study of extreme interest with regard to their approach to the problems of data handling and automated mapping, and in these respects I confidently commend this work to the wider readership beyond the shores of Britain. All those concerned with biological mapping should certainly make a point of examining this Flora; their interests are well catered for by introductory chapters that cover these aspects of the project. Regrettably its very high cost will place it beyond the reach of many interested British users (although it must be noted, a very generous pre-publication price was offered). If some aspects of the end product are less than completely successful, we should nevertheless have a real sense of gratitude for this most enterprising example of the application of modern techniques to a basic format hallowed by time and the activities of distinguished predecessors. There is much to be learnt from the Birmingham experiment in the difficult art of putting new wine into old bottles.—J. F. M. CANNON, Dept. of Botany, British Museum (Natural History), Cromwell Rd., London SW7 5BD.

Biology and Classification of Dwarf Mistletoes (Arceuthobium). By F. G. HAWKSWORTH and D. WIENS. 234 pp. U.S. Govt. Printing Office, Washington, D.C. 1972. \$4.50.

The long-awaited monograph of dwarf mistletoes has now appeared. It is a hard-cover book that, because of its professional appearance and low price, and through the fact that it is an official government publication, will undoubtedly be the standard handbook on the subject for decades. It therefore needs to be scrutinized and carefully evaluated at the outset, especially since its taxonomic conclusions are a drastic departure from most previous views. Much of the more important work has been previously published by the authors in various botanical journals.

The treatment begins with a brief introduction and historical sketch, after which the life cycle is followed through and general distributional summaries are provided. Host relationships are also treated in detail. Under the heading "Mechanisms and trends of evolution" we find factual information and exceedingly tenuous threads of argumentation in a blend that leaves me with a distinctly uneasy feeling. Among other things, the obvious is being rather overworked when we read (p. 36) that "The genetic system is presumably sexual and obligately out-crossing (the genus being dioecious)" and such statements as "But if hybrids do not occur, we could hardly expect to find literature on the subject."

Under the heading "Systematics of *Arceuthobium*" the taxonomic views of the authors are explained. It is by now clear that much of the writing that precedes the formal taxonomic treatment is preparatory to the more radical features of the latter. In the first systematics section the authors appeal to Danser's contention to the effect that the business of taxonomy is the classification of life cycles. Phenological data, therefore, are greatly emphasized. To anyone acquainted with the taxonomic practice of Danser the situation will seem very ironical, for Danser could hardly have anticipated that his views would lead to what has now happened to *Arceuthobium*. At any rate, the systematics section reads like an apologia, leading to expressions such as the following sentences: "Whether . . . differences are easily discernible in a particular specimen in no way affects their intrinsic taxonomic value. The distinctions between classification and ease of identification should not be confused". I may be forgiven if I feel that this clashes with the authors' expressed objective (p. 2) "to develop a useful, yet natural system of classification for *Arceuthobium*". It is fortunate for the working botanist that convenience does play a role in the taxonomic treatments of most of his colleagues.

The crucial item of the authors' "modus operandi" is perhaps expressed on pp. 41 and 42. They find no evidence of hybridization. While I do not need to be convinced of the possible significance of this, I am by no means convinced that intermediates between many of Hawksworth and Wiens' species could be easily spotted. This, and the morphological integrity of groups is taken to mean that they should be recognized as species. It is emphatically denied that the ecotype concept can be utilized; nothing but the species will do. It is nevertheless admitted that some of the dwarf mistletoes accorded specific rank "might correspond to regional ecotypes" to which the authors add, rather lamely ". . . but most taxonomists consider regional ecotypes to be comparable to subspecies so the taxonomic treatment would not be greatly different".

The results are spectacular. California, which in the evaluation of virtually everyone else in this century has had three species (*A. americanum*, *A. campylopodum*, and *A. douglasii*), now sports no fewer than nine. Even the taxon called by Gill *A. campylopodum* forma *typicum* yields two full-fledged species; Gill's forma *blumeri* is split into two more on the basis of what, I am sure, to most taxonomists will appear extremely trivial differences (p. 103). While western North America previously limped along on four species, this number has now shot up to 15.

The fundamental issue on which I disagree with the authors is their taxonomic judgment. It is no good to say that the mass of details that they have gathered supports their taxonomic concepts; it may support their contention that discontinu-

ities exist. But surely, discontinuity, even where demonstrated beyond a doubt, does not automatically compel us to place these groups at the specific level!

As Davis and Heywood write, in the context of taxonomic recognition of ecotypes: "The question that should be asked is what it is useful to recognize and for what purpose." Hawksworth and Wiens neither ask nor answer these two important questions. What can, indeed, be the purpose of formally recognizing and naming species that require so much sophisticated procedure to separate from one another? When a person (myself) who has worked in *Arceuthobium* for 15 years finds it impossible to distinguish between most of these new species, even with the aid of the detailed descriptions and illustrations provided, is there not something seriously wrong with that treatment?

I fear that the authors have "pulled a Trelease" in their systematic treatment. Anyone who has tried to use Trelease's monograph of *Phoradendron* will know what I mean—it is a publication that has done more harm than good in creating a vast number of new nomenclatural entities. Work in *Phoradendron* since that time has been plain hell, the fault being equally divided between *Phoradendron* and Trelease.

A comparison between the two generic treatments is by no means completely fair. Trelease's work brims with actual errors; infrageneric divisions are often quite meaningless and inconsistent, and its overall organization is dismal. No such faults can be assigned to the *Arceuthobium* treatment, which is clearly organized although I find the writing anything but smooth; most of the colored and black-and-white illustrations are good, some excellent. The detailed specimen citation and mapping also raise it far above *Phoradendron* level. Yet the overall effect, I am afraid, will be similar in that the great majority of Hawksworth and Wiens' "species" can be identified only by a few very highly trained people.

I should add that it is to the authors' great credit that they have, in previous publications, revived and/or discovered some very clearly marked Mexican species that were virtually unknown. With regard to those it is certainly extremely useful to have clear illustrations and textual analyses.

There are some unfortunate gaps. Three of the four extra-American species are neither illustrated nor mapped. While this may be understandable for the two Chinese species (I am by no means convinced that they are in any significant way different), an illustration and map of the type species, *A. oxycedri*, is a serious lack. While the title speaks of "Biology", there is no mention of the endophytic system, of hyperparasites, or the patterns of shoot-emergence from the host.

Some factual errors have also crept into the text and illustrations. The puzzling statement in the very first paragraph (and repeated in the generic description, p. 62) that the stems of *Arceuthobium* have no central vascular cylinder is perhaps traceable to a similar, vague statement in Gill's earlier monograph. The verticillate branching illustrated in Fig. 1D is quite erroneous; Fig. 2D shows an impossible sequence of young and older fruits; Fig. 3 does not illustrate a "cross-section" of the fruit as written in the legend.

One wonders also why such terms as chromatography, diploid, photoperiod, and many others need to be accommodated in a glossary. I wished the glossary, if deemed necessary, had been given more careful thought, as there are several questionable definitions. The definition of primitive taxa, for example, as "Plants that have characters also possessed by their ancestors", I find neither helpful nor defensible.

In summary, then, this monograph represents the accumulation of a vast amount of detail poured into a taxonomic mold that very few people will find usable. To a person acquainted with the genus at least north of Mexico, Hawksworth and Wiens' treatment is not designed to foster faith in computer analysis, chemotaxonomic approaches or—perhaps more fairly—in the authors' taxonomic judgment. Someone, at some future time, will have to sit down to very much the same information and try to come up with judgments in *Arceuthobium* that are more workable and meaningful than those of Hawksworth and Wiens.—JOB KUIJT, Department of Biological Sciences, University of Lethbridge, Alberta, Canada.

The Description and Classification of Vegetation. By DAVID M. SHIMWELL. xiv + 322 pp., 70 figs., 68 tables. Univ. of Washington Press, Seattle, and Sidgwick and Johnson, London. 1971. \$10.50.

Description of vegetation is an ecological tool, for all describers of vegetation have been interested in ecological relationships. The reverse is by no means true; nor is interest in other branches of botany, the botany of individual plants, for example, such as floristics, physiology, or morphology, a guarantee that the investigator will make the primary assumption of an ecological relationship between the phenomena he describes and the environment in which the phenomena are produced.

Classification becomes necessary in science just as soon as enough descriptive data are collected to make possible, and necessary, fruitful discussion and comparison, constructive criticism, and teaching (to paraphrase Pallmann). We evidently have enough descriptive data on vegetation now, since in fact for many areas there exist several vegetation classifications.

Shimwell's book is thus timely and valuable. However, it was written and published in Britain, for a British audience, using British examples, with attention to problems of British vegetation. This is not bad, only different. It does give a warped view of the subject. Still, British work on plant ecology has been outstanding and abundant. Work in floristics, history, many aspects of autecology, competition, experimental ecology, vegetation survey, pattern analysis, statistical methods applied to classification and ordination, and integration with soil properties is well-treated in Shimwell's book.

However, I think several concepts are not clearly presented. Chapter 1 on "Quantitative description of species populations" should be looked at logically and compared with similar material in other textbooks. Probably there *is* no operational definition of a species population. Shimwell's definition of an ecosystem is also non-operational, however beguilingly phrased in terms of niches. Quantitative methods of analyzing vegetation need systematization. I would prefer a system based on the properties measured: weight, cover, density, site index, layering, vitality, etc., with clear recognition of what the numbers attached to these parameters mean. Such non-absolute "measures" as frequency and importance value are then immediately seen to be expressed in peculiar units. Specifically any "point" method of recording the composition (cover, density?) of vegetation records frequency if the "point" has area (cf. Hutchings and Holmgren in *Ecology* 40(4):668-677, 1959). Additional useful methods should have been drawn from applied plant ecology-forestry, range management, agronomy.

Chapter 2 on units of vegetation classification traces genealogies of concepts such as association and formation in various local "traditions". Surely there is a modicum of agreement on these concepts now. Shimwell throughout his book emphasizes the plethora of opinions held by individual plant ecologists. More critical analysis of, or more selectivity among, these opinions would have been welcome. And to localize genealogies of ideas in this way is to peer into people's thoughts, conversations, reading, and to deny that a science is really a reticulate community.

Vegetation can be described and classified physiognomically, functionally, structurally, genetically, and floristically, and chapters are devoted to these methods. I would agree with the associates of Braun-Blanquet who point out that floristic knowledge leads into the other methods, but not vice versa. The others have what looks like a distinct advantage in requiring less botanical knowledge, but this is obviously a contradiction since vegetation is composed of plants. They also allow, even demand, the formation of deductive schemes of relationships. Such schemes are a very mixed blessing as Clements' successional straitjacket for American vegetation has shown. Shimwell gives a good presentation of the Braun-Blanquet methods, and this part of the book is extremely valuable. Perhaps it will lead to the simple and basic realization that data on vegetation must be collected systematically to describe any system of vegetation.

The next chapter on vegetation gradients and continua should have been tied to the preceding one on the Braun-Blanquet system. Both the collection and presentation of data that are subsequently arranged into continua have been poor. The data cannot be re-arranged. The best documented continua or gradients or ecological series of functional relationships are in work done by the Braun-Blanquet people or by the Russians. Shimwell neglects the Russian work completely, and no more serious mistake in vegetation description and classification could be made. The ecological series documented by Aleksandrova, Sukachev, Ramensky, Wendelberger, Braun-Blanquet himself, Gjaerevoll—to name only a few the reviewer has found useful in teaching—well illustrate vegetation as a factorial function of environmental factors.

Any new book treating the ecology of vegetation is useful. Shimwell's book is no exception. The field is multifarious, expanding rapidly, and there is no consensus on methods, techniques, even goals. Most techniques have not been tested widely. Shimwell's book makes teaching and learning the subject easier. It provides a convenient reference for students. It is not the only text a beginning student should have access to.—JACK MAJOR, Botany Department, University of California, Davis 95616.

Annual Review of Ecology and Systematics. By RICHARD F. JOHNSTON, PETER W. FRANK, and CHARLES D. MICHENER, Eds. Vol. 2, 1971. iv + 510 pp. Annual Reviews Inc., Palo Alto. \$10.

The general reader will be most pleased with this volume, the second in a projected series. On the other hand, plant systematists may find most of the "reviews" of only peripheral interest. The diffuse subject matter of this volume demonstrates the futility of attempting a review of such diverse fields as ecology and systematics and still have a product palatable to either specialty. To place together in one volume articles with titles as divergent as "The sacred in human evolution", and "High-latitude phytoplankton", will either broaden one's reading range or allow one to decide that the few pertinent articles do not justify the purchase of the book and especially not the whole series. Perhaps this difficulty could be alleviated by tailoring alternate volumes for particular readerships.

Among the 19 papers in this issue, 4 contained information of special interest to this reviewer. These were "Adaptive radiation of reproductive characteristics in angiosperms. II: seeds and seedlings" by G. Ledyard Stebbins; "The karyotype in systematics" by Ray C. Jackson; "Arctic and alpine plant life cycles" by Lawrence C. Bliss; and "Seed predation by animals" by Daniel H. Janzen. These are the articles most allied to higher plant systematics, but one is immediately aware from the titles alone, that they are hardly in the main stream of systematic botany.

Stebbins' article is the second in a series that illustrates his thesis that the characters employed by evolutionary biologists in deducing relationships and in erecting systems of classification are expressions of adaptation to particular environmental pressures, and not products of orthogenesis. Seeds and seedlings are crucial stages in the life histories of plants where integration and coordination of morphogenetic events, physiological processes, and morphological form are indispensable and where selection is likely to have a strong influence in molding unique qualities of populations. Successful reproduction and establishment often present conflicting demands upon the organism so that evolutionary compromises, for example, between seed size and number, often result. The adaptive significance of many properties of seeds and seedlings is pointed out based upon gleanings from the meager scattered literature and made cohesive with numerous personal observations by the author.

While Stebbins' paper utilizes only a modest bit of the biological literature, Jackson marshals 174 mostly recent references to update karyotype study as applied to systematics. Only a few years ago one could ascertain the karyotype of an organism by counting the chromosomes, measuring their relative and absolute arm lengths,

and noting the occurrence and distribution of secondary constrictions and perhaps associated satellites. Jackson notes that a dozen dimensions are available for a modern karyotype description and observes that new ones continue to be developed. Most of the new approaches utilize developments of molecular biology. His article concludes with an interesting consideration of karyotype evolution interpreted in the light of these newer developments.

Arctic and alpine plant life cycles are admirably described by Bliss. These biomes occupy about 15% of the earth's land surface, and occurring as they do at both ends of the earth and upon the higher mountains even near the equator, present uniquely interesting problems in plant evolution and systematics. Bliss' treatment of the ecology of these regions is an excellent basis for contemplating the evolutionary problems presented by their floras. From the simplest generalizations we are led gently from region to region and into the complexities of tundra community dynamics and on to ecological strategies of particular tundra species. This is one article likely to become well-worn through consultation of the vast amount of information it contains.

Studies of co-evolutionary relationships of plants and animals are receiving attention from increasing numbers of students. Janzen's summary of aspects of seed predation by animals is thus of special value. Although written from the zoological standpoint, it complements well Stebbins' article cited above and also the paper of Harper, Lovell, and Moore that appeared in volume 1 of this series. (*Ann. Rev. Ecol. & Syst.* 1, 1970). The intricate interactions described by Janzen serve admirably to point up opportunities for research in this enormous subject while also showing the pitfalls of naive interpretations of observations.—DALE M. SMITH, Department of Biological Sciences, University of California, Santa Barbara 93106.

A Classification of the Eucalypts. By L. D. PRYOR and L. A. S. JOHNSON. 102 pp. The Australian National University, Canberra. 1971. (Available from International Scholarly Book Services, P.O. Box 4347, Portland, Oregon 97208, \$3.95, softbound.)

The authors present a summary of their goal of almost two decades—a critically assessed and interpreted new classification of the eucalypts, one which integrates the findings of all workers, and not just their immediate colleagues.

After briefly reviewing both old and new classifications, the authors review the types of characters employed in their "(nonnumerical) phenetic" classification. These include various morphological features, but especially characters of the inflorescence, opercular structure, and ovule and seed coat structure. Evidence from chemistry, biotic associations, and genetics also has been considered.

In an interesting approach to describe stages in the process of evolution in changing environments, the authors recognize seven variation patterns, including one referred to as "Phantom". This last is a term originally proposed by Brett to describe a situation where a formerly widespread parent species has disappeared, leaving only traces of itself in the form of deviant disjunct populations. After giving examples of each of these patterns in *Eucalyptus*, a discussion of generic limits ends with the authors' decision not to recognize separate, segregate genera.

The above is presented in twenty pages, while the remainder of the text is devoted to the actual classification. The present volume does not include formal, nomenclatural changes. What does appear is an infrageneric classification that "... follows a rationalized plan explicitly divorced from the traditional system embodied in the International Code of Botanical Nomenclature". This is effected by assigning a code name of 1-6 letters to each taxon. Thus the code for *Eucalyptus parramattensis* is SNECF, S for subgenus *Symphomyrtus*, N for section *Exsertaria*, E for series *Tereticornes*, C for subseries *Bancroftinae*, and (finally!) F for the species *E. parramattensis*.

Readers might take either of two extreme positions: this is a weird, useless code that is taxonomic fallout from the computer age; or, this may be a useful procedure since it summarizes a great deal of detailed taxonomy in a few alphabetical letters. I can sympathize with both views. As the authors point out, a similar coding approach was suggested five years ago by David Hull in *Systematic Zoology*. Except where an abbreviation is needed for data accumulation in the field, many former supporters of such a system no longer champion it strongly. Why? Because its only advantage was when much electronic information retrieval was restricted to the limits of the 80-column computer card. The third and fourth generation computers available today at most universities and research institutes (at least in the United States) handle alphabetic information retrieval tasks in a way that was rarely possible in the early days (five to ten years ago!). Coding is no longer necessary.

My point is, that while the proposed coding scheme possesses more information than just a binomial, it also is much more cryptic than a binomial. If one has to look up the code for the full hierarchical classification of a species, he might rather just look at the classification with all taxon names fully spelled out.

To summarize, the authors obviously devoted considerable time to the creation of a taxonomic code. It should prove useful as a shorthand notation *within* a computer, but it is not essential for sophisticated information retrieval. The systematist still probably will always use the binomial to retrieve information. When he wants more insights into taxonomic relations, he probably will still refer to the noncoded columns of Pryor and Johnson's classification.—THEODORE J. CROVELLO, Department of Biology, University of Notre Dame, Notre Dame, Indiana 46556.

Tremellales. By BERNARD LOWY. 153 pp., illustrated. Flora Neotropica Monograph No. 6. Hafner Publishing Company, Inc., New York. 1971. \$12.95, paper bound.

In his introduction to the monograph, Prof. Lowy recounts the history of botanical exploration of Tropical America during the 18th and 19th centuries with emphasis on mycological endeavours, and he sets forth his goal, which is not only to describe all tremellalean fungi that reliably have been reported for the region extending roughly to the 23rd parallels north and south of the equator but also to provide keys that will enable students to identify these fungi. Also discussed are the general characteristics of the Tremellales, phylogenetic relationships, methods of study, geographical distributions, and sources of material examined in preparing the monograph.

The second section of the study, Taxonomic Considerations (reproduced with minor changes from *Taxon* 17:118–127, 1968), provides a brief analysis of the taxonomic history of the Basidiomycetes from the classic macromorphologic system of classification of Fries to the micromorphologic system pioneered by Patouillard late in the 19th century. Patouillard (and Brefeld, independently) was the first to emphasize the fundamental importance of the basidium and he recognized two major groups of Basidiomycetes, the Hétérobasidiés, having septate basidia, and Homobasidiés having nonseptate basidia. Lowy discusses in greater depth the problems introduced into the classification of the Heterobasidiomycetes by genera such as *Tulasnella*, *Gloeotulasnella*, *Ceratobasidium*, *Cerinomyces*, and others, which possess characteristics that deny their being allied unequivocally with either the subclass Heterobasidiomycetidae or the subclass Homobasidiomycetidae. After a lengthy evaluation of the ideas of other students of these fungi, the author defends the establishment of a third subclass, Metabasidiomycetidae, to encompass those taxa (1) having an incompletely divided or aseptate basidium with swollen or notably enlarged sterigmata, (2) producing basidiospores germinating by repetition or by production of conidia, and (3) forming basidiocarps that may or may not be waxy or gelatinous. The more narrowly defined Heterobasidiomycetidae includes taxa having completely divided basidia with swollen or notably enlarged sterigmata,

producing basidiospores germinating by repetition, and forming basidiocarps that usually are waxy or gelatinous in texture. The Homobasidiomycetidae, not treated in the monograph, includes all other Basidiomycetes, i.e., Aphyllophorales, Agaricales, and Gasteromycetes, which have undivided basidia lacking notably enlarged or swollen sterigmata, have basidiospores not germinating by repetition, and have mostly nonwaxy and nongelatinous basidiocarps.

The Systematic Treatment embraces five families of Heterobasidiomycetidae (Auriculariaceae, Hyaloriaceae, Phleogenaceae, Sirobasidiaceae, and Tremellaceae) classified in the order Eutremellales, and three families of Metabasidiomycetidae (Ceratobasidiaceae, Dacrymycetaceae, and Tulasnellaceae) in the order Metatremellales. Forty genera and one subgenus including 144 species and four varieties are characterized and synonymies given. Keys to the families, genera, and species are provided. Basidial, sporal, and hyphal characteristics of representative species of 20 genera of the eight families are illustrated by line drawings in 24 plates; basidiocarps of representatives of six genera are pictured photographically in five plates; and eight maps depict the geographical distribution of all species described in the text. A list of three excluded and 26 incompletely known species is appended.

Literature citations (136 references) and a general index complete the volume.—RICHARD K. BENJAMIN, Rancho Santa Ana Botanic Garden, Claremont, California 91711.

Experimental Studies on the Nature of Species V. Biosystematics, Genetics, and Physiological Ecology of the Erythranthe Section of Mimulus. By W. M. HIESEY, M. A. NOBS, and O. BJORKMAN. vi. + 213 pp. Carnegie Institution of Washington, Washington, D.C. 1971. \$6.75 (paper).

This well written monograph is the latest volume of the now classical series, *Experimental Studies on the Nature of Species*. The basic questions that the current authors pose vary little from those asked in the earlier volumes. However, the development of insights into the actual substance of the questions over the last several decades and the employment of new research techniques (particularly for the analysis of morphological data as well as for the critical measurements in the physiological studies) have resulted in a meaningful and highly informative study.

The study is divided into four main sections: Biosystematic Relationships within the *Erythranthe* section of *Mimulus*, Genetic and Transplant Studies, Comparative Physiological Studies on Ecological Races and Species, and Growth of Excised Tissues of *Mimulus* under Aseptic Conditions. The fifth section is a short history of the levels of approach in the study of the nature of species as well as a discussion of the direction future studies will take.

From the biosystematic data it has been established that sect. *Erythranthe* is divided into two species complexes, *M. cardinalis-lewisii* and *M. verbenaceus-east-woodiae-nelsonii*. Further, genetic and transplant studies involving the use of morphological and physiological characters have shown that within these complexes the populations comprising each species possess definite genetic similarities. However, the data also indicate that real genetic differences between populations and races of a particular species exist alongside these genetic similarities.

The comparative physiological studies should be particularly mentioned. A set of factors (e.g., light intensity, CO₂ concentration, and temperature) that affect the photosynthetic rate were investigated in great detail and with great precision in *Solanum*, *Atriplex*, and *Solidago* as well as in *Mimulus*. The net result of this work is the emergence of an understanding of alternate modes of physiological differentiation in response to environmental diversity. With the publication of this monograph the future direction of this Carnegie group may be clearly seen.—DENNIS R. PARNELL, Department of Biological Sciences, California State University, Hayward 94542.

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A TAXONOMIC RE-INTERPRETATION OF THE OROBANCHE CALIFORNICA COMPLEX

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Considerable difficulty has been encountered in classifying plants treated by Beck (1930) and Munz (1930) as *Orobanche californica* and *O. grayana*. Sporadic inconstancies in nearly all morphological characters result in puzzling variation patterns and combinations of features that form groups that are not readily defined taxonomically. This complexity has led me to make a taxonomic re-evaluation of these groups. Moreover, a study of collections made since 1930, as well as of type specimens available to me but not seen by either Beck or Munz, suggests changes in both the taxonomy and nomenclature of these plants.

The plants treated here belong to **Orobanche** L. sect. **Nothaphyllon** (A. Gray) Heckard, comb. nov. [Basionym: *Aphyllon* Mitchell sect. *Nothaphyllon* A. Gray, Bot. Calif. 1:584. 1876. Lectotype species here designated: *Aphyllon californicum* (C. & S.) A. Gray = *Orobanche californica* C. & S.]. This section, a small but widespread group of American species, was previously called *Orobanche* L. sect. *Myzorrhiza* (Phil.) Beck (Bibl. Bot. 4:78. 1890) on the erroneous assumption that the genus *Myzorrhiza* Philippi (Linnaea 29:36. 1858) established priority for the sectional name.

In my judgment the plants treated as two species, *Orobanche californica* and *O. grayana*, by Munz and by Beck comprise four species. The relative distinctness of one of these four, *O. corymbosa* (Rydberg) Ferris of the Great Basin, was pointed out by Ferris (1958) when she gave specific rank to *O. californica* var. *corymbosa* (Rydb.) Munz. This species is not treated further in this paper except in the key to species. My recognition of a second species, *O. parishii* of southern California and environs, is reflected in the raising of *O. californica* var. *parishii* Jepson to specific rank. I propose two subspecific taxa to encompass its geographic variants. Treatment of the remaining two species involves nomenclatural changes owing to a reinterpretation of the type specimens as well as to changes in taxonomic circumscription. One of these species is a widespread and morphologically complex species with six subspecies in the western United States and contiguous areas, and the other is a monotypic species confined to California. The widespread, variable species has heretofore been called *O. grayana* but should properly be named *O. californica*. The other species previously called *O. californica* must have a new name and I have selected *O. vallicola*.

My revision has been based on herbarium specimens and living specimens, when available. *Orobanche* is often difficult to find in the field, although searching at localities listed on herbarium labels was in some instances successful. The plants are becoming increasingly scarce with the spread of man's activities. In order to document the occurrence of these rare plants I am citing one specimen from each of the known localities.

Chromosome counts in this group (Chuang & Heckard, in prep.) are mostly $n = 24$, but $n = 48$ has appeared in two species, *O. corymbosa* and *O. parishii*, indicating that polyploidy may be one of the causes of taxonomic difficulties.

Thieret (1971) pointed out that the biology of most Orobanchaceae is poorly known and even such basic information as the hosts for these parasitic plants is seldom noted by collectors. From the host data assembled in this study there appears to be some host specificity for the species recognized here. Indeed, this difference is one of the reasons for retaining *O. californica* and *O. vallicola* as distinct species. While *O. vallicola* is frequently reported growing on the roots of trees and shrubs, *O. californica* is chiefly reported on herbaceous perennials, largely of the Compositae. Occasional reports of *O. californica* on various plants other than those of the Compositae need confirmation. There is some evidence of host specificity at the subspecies level within *O. californica* as is indicated under each subspecies.

TAXONOMIC CHARACTERS

Formulating a taxonomy for the species of this complex is hindered by the limited number of morphological features available for comparative purposes and by the sporadic inconstancy of most of these features.

The characters used in this study, except for overall sizes, are all in the inflorescence or flower. Significant differences in plant size do exist and involve independent variation in length of stem and inflorescence. Vertical measurements are given in this paper in terms of length rather than height in order to avoid any confusion with the above-ground height. The entire stem and often the lower portion of the inflorescence remain below ground.

Associated with plant size are differences in inflorescences (figs. 1, 2) that are of diagnostic value. These differences are only of degree and are modifications of a general branched (paniculate) inflorescence (fig. 1, M). Failure of the branches to develop on the main axis results in a simple racemose or spicate inflorescence (fig. 1, N) and this may occur within the same population or even in the same plant on a second stem arising from the base of a cluster. Whether the simple inflorescences are racemose or spicate is problematical since the flowers are usually sessile (at the top) and pedicelled (at the bottom) in the same inflorescence. Occasionally either the sessile or pedicelled condition is present exclusively in an inflorescence. This is especially true for *O. vallicola*, in which both conditions as well as the mixed one are present. The term subspicate has been used in this paper to describe the inflorescence that

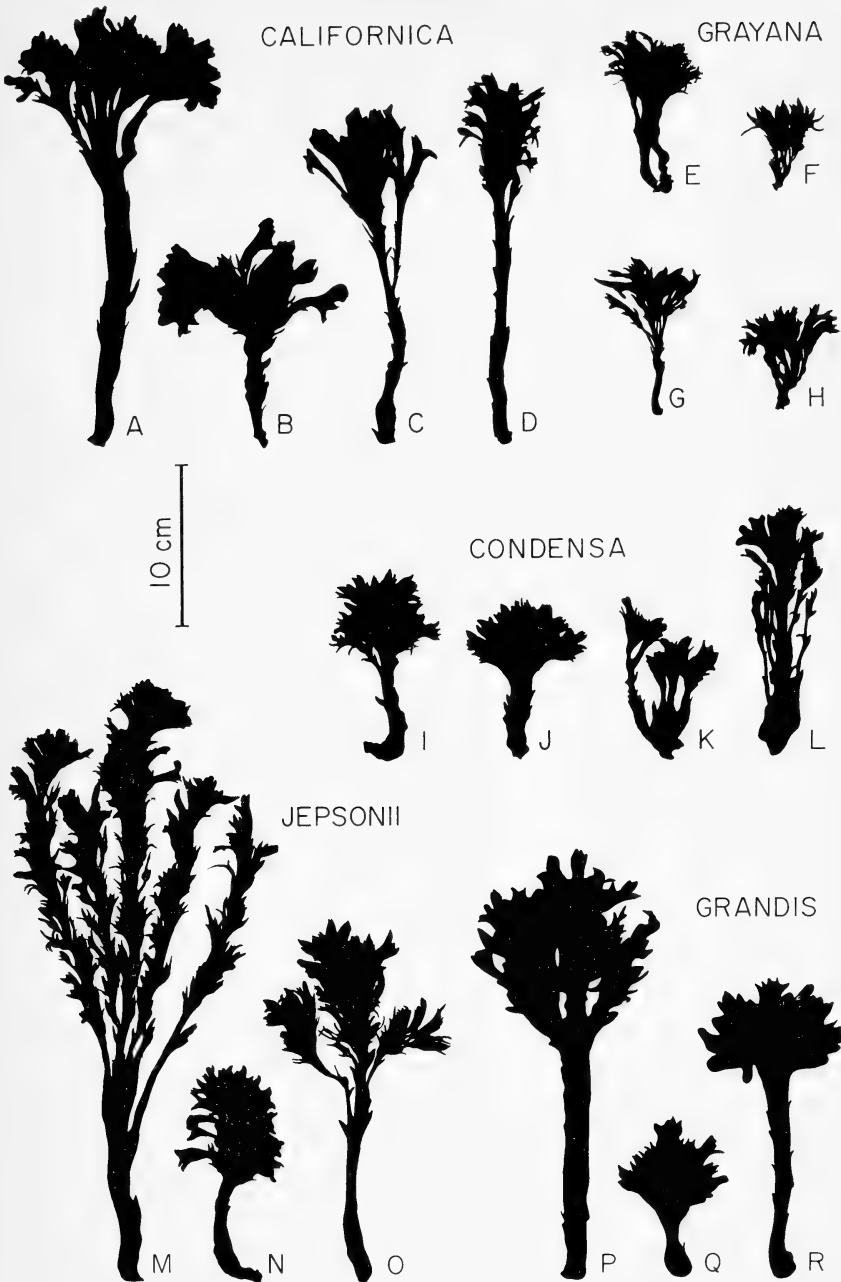


FIG. 1. Silhouettes of herbarium specimens of *Orobanche californica* showing habit and size. A-D, ssp. *californica*. A, Roderick in 1961; B, Setchell in 1909; C, Setchell in 1908; D, Otis 2350. E-H, ssp. *grayana*. E, F, Suksdorf in 1882; G, Nutting in 1915; H, Beans in 1914. I-L, ssp. *condensa*. I, Lee 1055; J, Bacigalupi 5242; K, Condit in 1910; L, Bacigalupi 5128. M-O, ssp. *jepsonii*. M, Chandler in 1905; N, S. G. Smith 2658; O, Brewer 1273. P-R, ssp. *grandis*. P, Wood in 1946; Q, Hoffmann in 1930; R, Pollard in 1954.

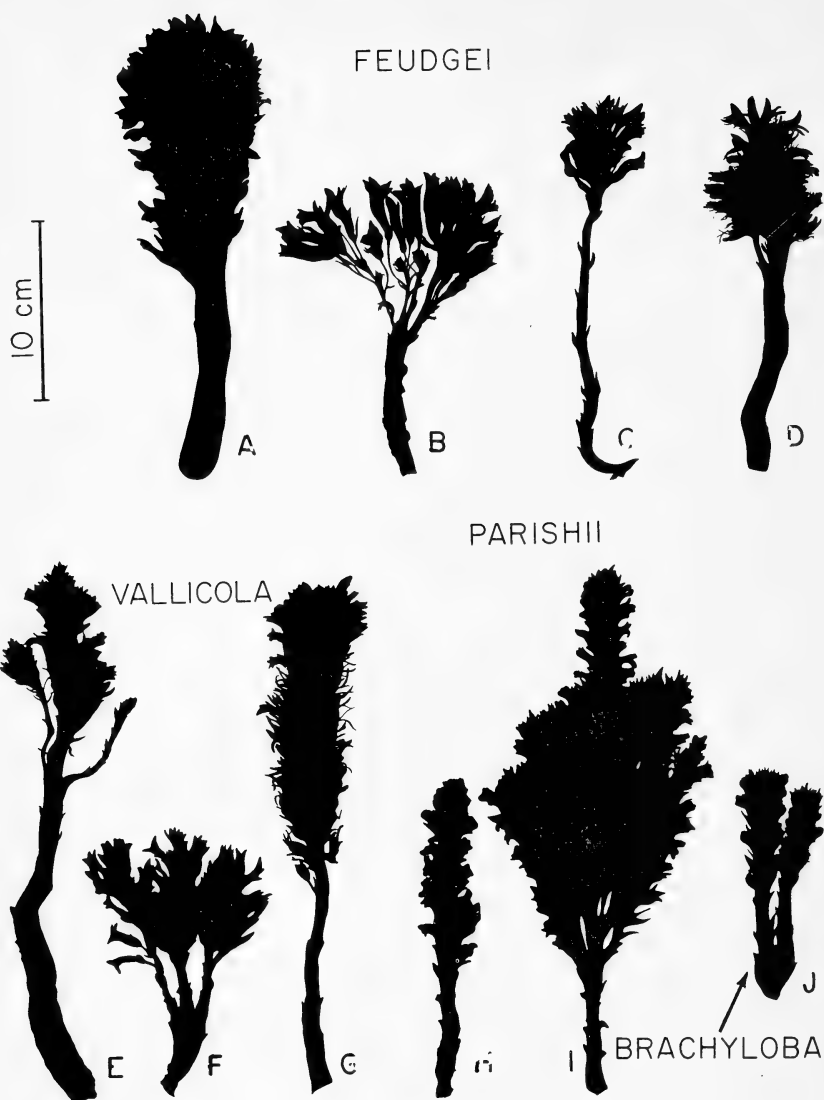


FIG. 2. Silhouettes of herbarium specimens of the *Orobanche californica* group showing habit and size. A–D, *O. californica* ssp. *feudgei*. A, *Breedlove* 4010; B, *Hall* 6327; C, *Munz* 5827; D, *Abrams & McGregor* 654. E–G, *O. vallicola*. E, *Barber* in 1898; F, *Murphey* in 1946; G, *Jepson* 6196 (holotype). H–I, *O. parishii* ssp. *parishii*. H, *T. Brandegee* in 1894; I, *Davidson* in 1889. J, *O. parishii* ssp. *brachyloba*, *Raven & Thompson* 20794 (holotype).

has both sessile and pedicelled flowers. This inflorescence is characteristic of both *O. vallicola* (fig. 2, G) and *O. parishii* (fig. 2, H). The inflorescence of both these species (fig. 2, E, F, I) may also be branched

and thus "paniculate", as is that of *O. californica* ssp. *jepsonii* (fig. 1, M, O), but the latter often has the branches racemose rather than subspicate. Another variation in the inflorescence involves a greater elongation of the pedicels of the lowermost flowers along with a shortened inflorescence and results in the subcorymbose inflorescence characteristic of *O. californica* ssp. *grayana* (fig. 1, E-H). This inflorescence is present along with subspicate ones in ssp. *californica* (fig. 1, A-C), ssp. *feudgei* (fig. 2, B), and ssp. *grandis* (fig. 1, Q-R). When the paniculate or racemose inflorescence is both reduced and congested, it is described as subcapitate, as in ssp. *condensa* (fig. 1, I, K).

Bract shape and the number of parallel veins of the bract are useful features for distinguishing *O. parishii* from *O. vallicola*. The bracts of *O. parishii* (fig. 3, L-N) are ovate to lance-ovate and have seven or more conspicuous parallel veins, while those of *O. vallicola* (fig. 3, I-K) are lanceolate and have about five or less veins. In herbarium material, the bracts of *O. parishii* are lighter in color and the veins are much more conspicuous, which may indicate a thinner bract. The bract of *O. californica* (fig. 3, H) is usually broader than that of *O. vallicola* but similar in venation pattern.

Flower characters (fig. 3, A-G) useful in taxonomy are: color; size of parts, especially length of corolla and lips; shape of corolla lobes, especially whether the apex is rounded or pointed; degree of spreading of corolla lips; and shape of stigma. The stigma varies in thickness, in degree of development of the bilobed condition, and in degree of outward curvature of the apex and margins of the lobes. Spreading lobes that are not rolled outward at the margins (infundibular) characterize *O. californica* (fig. 4, D, F), although sporadic variants (fig. 4, A, B) in ssp. *californica* have the margins rolled downward (crateriform). The strongly bilobed stigma with conspicuously curved lobes is diagnostic for *O. vallicola* (fig. 4, J-L). The stigma of *O. parishii* (fig. 4, G-I) is somewhat infundibular or occasionally has curved margins.

REINTERPRETATION OF THE TYPE OF OROBANCHE CALIFORNICA

The type specimen of *Orobancha californica* Chamisso & Schlechtendal is a single, reduced, and fragmentary plant collected in October 1816 in the vicinity of San Francisco. The type is more similar to coastal bluff plants than to inland plants in the following features: 1) the corolla of the type is dark reddish-brown while in inland plants it is much lighter; 2) the corolla is tougher, thicker, and less brittle in the type than in inland plants; 3) the dimensions of the corolla (23 mm long with lips up to 10 mm long) are within the lower part of the range of coastal bluff plants but slightly exceed the usual lip length of inland plants, and the upper lip and lobes are broader than in inland plants; 4) the anthers are moderately heavily villous, an exceptional condition in inland plants. Therefore, I disagree with the current practice of applying the name *O. californica* to inland plants, for which I propose the name *O. vallicola*.

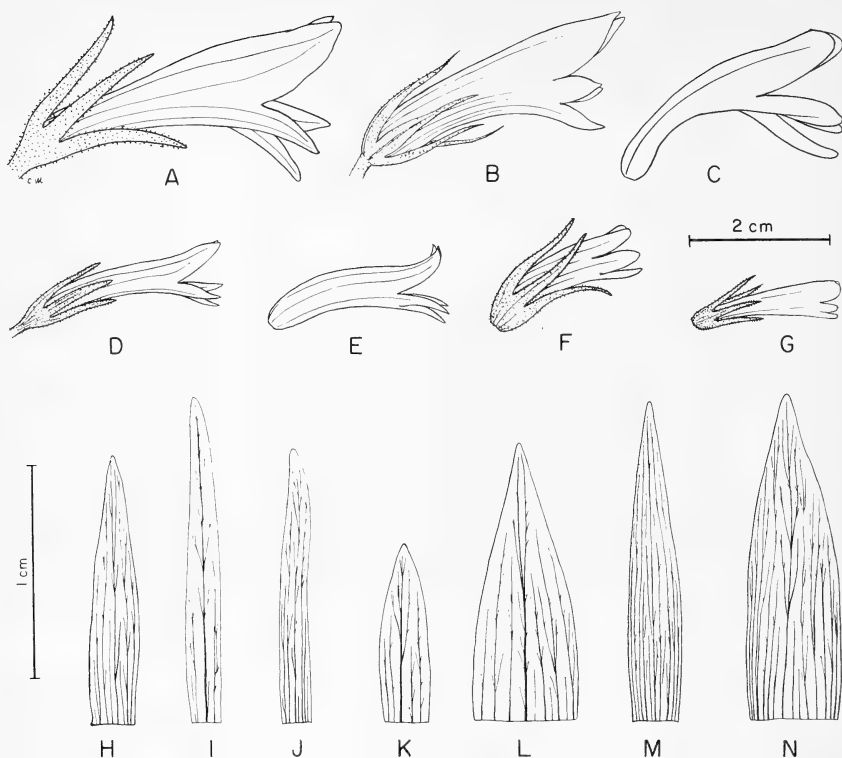


FIG. 3. Flowers (A-G) and bracts (H-N) in the *Orobanchaceae californica* group: A-G, *O. californica*. A, ssp. *grandis* (Pollard, holotype); B, ssp. *feudgei* (Munz 5827); C, ssp. *californica* (Roderick in 1961). D-E, *O. vallicola* (D, Kessell, 16 Sep 1956; E, Lile, 1 Oct 1933). F-G, *O. parishii*, F. ssp. *parishii* (Pierson 416); G, ssp. *brachyloba* (Raven & Thompson 20794). H, *O. californica* ssp. *jepsonii* (Chandler, holotype). I-K, *O. vallicola* (I, Crawford 547; J, Jepson, holotype; K, Murphey, 16 Oct 1946). L-N, *O. parishii*. L-M, ssp. *parishii* (L, Clokey 5308; M, Gander 286); N, ssp. *brachyloba* (Raven & Thompson 20794).

Orobanchaceae californica should instead be applied to coastal bluff plants, which heretofore have been called *O. grayana* var. *violacea* (Eastw.) Munz.

Munz (1930) was probably misled in his interpretation of *O. californica* by Chamisso and Schlechtendal's erroneous description of the anthers as sparingly or moderately villous. Actually the anthers of the type are quite villous with the hairs concentrated mostly along the dehiscence suture but also present on the back of the anther. Certainly the anther indument is well within the range of that in coastal bluff plants, but it would be an extreme condition or exception for *O. vallicola*.

The one feature of the type specimen that is more typical of *O. vallicola* than of coastal-bluff plants is the crateriform stigma with revolute

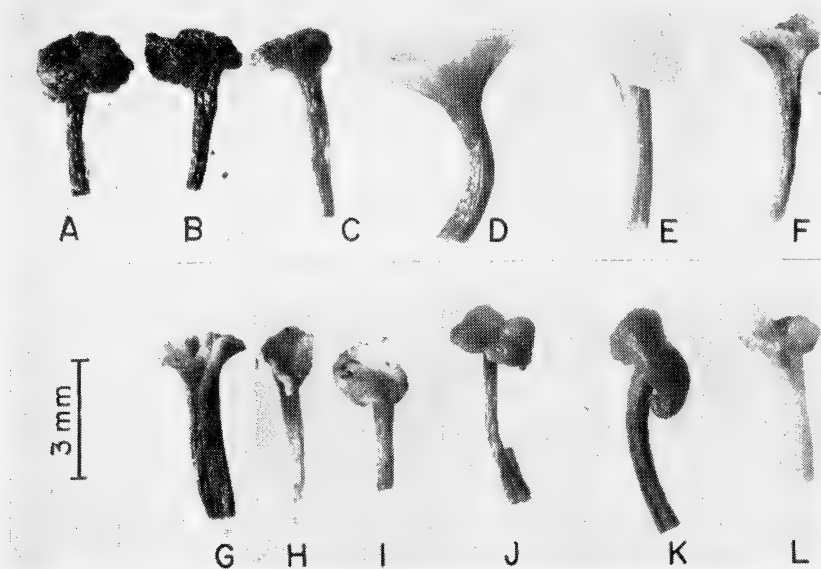


FIG. 4. Stigma types in the *Orobanche californica* group. A-C, *O. californica* ssp. *californica*. A, Eastwood in 1900 (isotype of *Aphyllon violaceum*); B, Chamisso & Eschscholtz, Oct 1816 (holotype of *O. californica*); C, Crampton 5915; D, *O. californica* ssp. *feudgei*, Holmgren & Reveal 2598; E, *O. californica* ssp. *grandis* (Norris in 1968); F, *O. californica* ssp. *jepsonii*, Chandler (isotype of *O. grayana* var. *jepsonii*). G-I, *O. parishii* ssp. *parishii*; G, Davidson, Aug 1899; H, Johnston 1762; I, Alderson 8327. J-L, *O. vallicola*. J, Jepson 6169 (isotype of *O. comosa* var. *vallicola*; K, Kessel in 1966; L, Crawford 547 (isotype of *O. californica* var. *claremontensis*).

margins (as in fig. 4, J-K). Stigma shape, however, is variable in both species and this stigma type is occasionally encountered in the coastal bluff form (fig. 4, A, C).

Attempts to re-collect an *Orobanche* similar to the Chamisso plant in San Francisco have not been successful. There is no apparent reason why plants similar to the Chamisso collection should not be found in suitable habitats around the ocean bluffs of San Francisco. Similar plants grow on coastal bluffs within 25 km to the south and 50 km to the north. On the other hand, the nearest collection of *O. vallicola* is in Marin Co. about 30 km north of San Francisco and in a less maritime environment.

TAXONOMY AND DISTRIBUTION

It is important to preface a taxonomic treatment and identification keys for this group of *Orobanche* with a word of caution concerning the perplexing variability in the group. There is an inconstancy in the inflorescence and floral characters that are used in formulating a taxonomy for these plants. Natural units, morphologically, ecologically, and geo-

graphically defined, do exist, but sporadic inconstancies may occur within these units in an entire population or portion of one. These variations result in overlap of the diagnostic characters separating the taxa and cause difficulty in formulating keys that will identify all the variant plants of a taxon. The keys of this treatment are constructed to account for some of this variation but not all, and plants exceptional in any one feature may be encountered.

The relationship of the considerable variability of these *Orobanche* to their parasitic habit is problematical. Ernst (1972) suggested in the case of hemiparasitic plants that parasitism may expand opportunities for survival and sympatric occurrences. Extension of the life expectancy of plants with reduced or marginal fitness could enrich their genetic and morphological diversity. Ernst's conclusion that taxonomists might be well advised to accept broader patterns of variation in superficial morphology for hemiparasitic plants should be valid also for holoparasites.

KEY TO THE SPECIES OF THE OROBANCHE CALIFORNICA COMPLEX

Corolla 2.5–5.0 cm long; corolla lips 10–14 mm long, widely spreading;

British Columbia to N Baja California, mostly in or W of the Cascade-Sierra-Peninsular ranges 1. *O. californica*

Corolla 1.5–2.5 cm long; corolla lips 4–10 mm long, erect to spreading.

Inflorescence spicate; upper corolla and lips white, yellow, pinkish, or buff, often with deep reddish or purplish veins; anthers glabrous or villous mostly along the dehiscent margins; California and Baja California.

Corolla lobes acute with mostly pointed apices; cauline bracts lanceolate with 5 or fewer inconspicuous parallel veins, dark brown in dried specimens; cismontane California from Trinity Co. S to Los Angeles Co. 2. *O. vallicola*

Corolla lobes obtuse with rounded to blunt apices; bracts ovate to lance-ovate with more than 5 conspicuous parallel veins, light brown or buff in dried specimens; Southern California and Baja California 3. *O. parishii*

Inflorescence corymbose or subcorymbose (becoming spicate in the Columbia Plateau); upper corolla and lips purplish on inner surface, paler and grayish on exterior; anther surface densely villous; sagebrush areas, Great Basin and Columbia Plateau and environs *O. corymbosa* (not treated)

1. *OROBANCHE CALIFORNICA* Chamisso & Schlechtendal, *Linnaea* 3:134. 1828. *Phelipaea californica* (C. & S.) G. Don, *Gen. Hist. Plants* 4:632. 1838. *Aphyllon californicum* (C. & S.) Gray, *Bot. Calif.* 1:584. 1876. *Myzorrhiza californica* (C. & S.) Rybd., *Bull. Torrey Bot. Club* 36:695. 1909. TYPE: “. . . e vicinia portus St. Francisci Californiae . . .”, Chamisso & Echscholtz. (HOLOTYPE: LE!; Photograph, JEPS).

Plants 4–35 cm in length, only the inflorescence above ground, the

subterranean stem portion 1–15 cm long; stems solitary to fastigiate branched, slender to stout (5–20 mm in diameter), bearing broadly ovate to subulate scales mostly less than 10 mm long; host attachment consisting of a few coralloid strands, only rarely forming an irregular bulbous mass; inflorescence subcorymbose or subspicate to racemose, glandular-puberulent throughout; pedicels mostly well-defined below, decreasing in length upwards in the inflorescence from 1–4 cm above to 0–1 cm in length, bearing 2 opposite or variously placed linear-subulate bractlets 5–10 mm long; calyx with subulate to linear-subulate, gradually attenuate lobes, 6–20 mm long; corolla strongly bilabiate, 22–45 mm long, white to pale rose and deep purple with yellow palatal folds, sparsely to moderately glandular-puberulent externally; corolla lips mostly widely spreading, 8–15 mm long, the upper lip usually slightly longer than the lower lip; lobes of upper lip deltoid to broadly deltoid with bluntly acute or rounded apices; lower lip parted into 3 lanceolate lobes; corolla tube arching forward placing the throat in a horizontal position; anthers densely villous, especially along the dehiscence suture, rarely glabrous; stigma variable in size, mostly with triangular, widely spreading to revolute lobes; capsule ovoid to cylindric-ovoid, 10–12 mm long; seed cuneiform, favose-reticulate, 0.4–0.6 mm long.

Hosts: Various perennials, chiefly of the Compositae (see each subspecies for specific hosts).

DISTRIBUTION: In and west of the Cascade-Sierra Nevada-Peninsular ranges from Vancouver Island, British Columbia, S to the Sierra San Pedro Martir in Baja California (fig. 5). Elevation 0–2,400 m.

Formulating an infraspecific classification of *O. californica* is impeded by the considerable variability in the rather few morphological features that must be relied upon for taxonomic delimitation and by sometimes baffling disjunction in the distribution of the variants. There is clearly a series of geographic variants that deserves taxonomic recognition, however, and this treatment attempts to point out the most significant of these by according them subspecific status. Subspecific delineation is based on features of habit (fig. 1, 2); corolla color, size, and shape (fig. 3); and to a lesser degree host preference. Anomalies in morphology or distribution and attendant problems in creating a workable classification are discussed with the appropriate subspecies.

KEY TO SUBSPECIES OF OROBANCHE CALIFORNICA

- Upper corolla tube and lips dark violet; calyx lobes, pedicels, and bracts violet-tinged, drying blackish purple; coastal dunes and hills from the Monterey Peninsula, California, N to southwestern British Columbia. la. ssp. *californica*
- Upper corolla tube and lips white or yellowish to pinkish or purple-tinged, often with the veins pink or lavender; calyx lobes, pedicels, and peduncles pallid to pinkish-tinged, drying brown; mostly inland from Baja California to the Cascade Range of southern Washington.

Corolla lips whitish to pinkish (reddish brown in herbarium specimens); corolla tube broad, 4 mm or more in diameter at the constriction and gradually widening toward the throat; montane in Baja California and Southern California to Ventura and Kern Cos. lf. ssp. *feudgei*

Corolla lips white or yellowish to pinkish (sometimes purplish-tinged in herbarium specimens); corolla tube slender below, usually less than 4 mm in diameter at the constriction and abruptly expanding distally toward the widely spreading lips.

Corolla 35–40 mm long; throat of corolla 10 mm or more in diameter; lower lobes of corolla lance-ovate, 5 mm or more broad; mostly near the coast, Los Angeles to San Luis Obispo Cos. le. ssp. *grandis*

Corolla 25–35 mm long; throat of corolla less than 10 mm in diameter; lower lobes of corolla lance-subulate to lance-oblong, usually less than 5 mm broad.

Plants usually longer than 10 cm; stem below the inflorescence 6 cm or more long; inflorescence racemose to paniculate; racemes 5–20 cm long; Central Valley of California and surrounding mountains to 3,000 m; occasionally in the Coast Ranges and their valleys. lc. ssp. *jepsonii*

Plants usually less than 10 cm long; stem below the inflorescence usually less than 6 cm long; inflorescence of subcorymbose or subcapitate clusters mostly less than 6 cm long.

Stem below the inflorescence usually less than 3 cm long; lower lobes of corolla lance-subulate, less than 3 mm broad near base, with acute and pointed apex; meadows of the Sierra Nevada and Cascade Range from Tuolumne Co., California, N to Klickitat Co., Washington; occasional in lowland meadows. lb. ssp. *grayana*

Stem below the inflorescence 3–6 cm long, lower lobes of corolla 3 mm or more broad, lance-oblong to narrow-triangular, with the apex blunt-acute or obtuse; South Coast Ranges from northern Santa Barbara Co. N to southern Santa Clara Co., California. ld. ssp. *condensa*

1a. *OROBANCHE CALIFORNICA* C. & S. ssp. *CALIFORNICA*.

Aphyllon violaceum Eastw., Zoe 5:85. 1900. *Myzorrhiza violacea* (Eastw.) Rydb., Bull. Torrey Bot. Club 36:695. 1909. *Orobanche comosa* var. *violacea* (Eastw.) Jeps., Man. Fl. Pl. Calif. 952. 1925. *Orobanche grayana* var. *violacea* (Eastw.) Munz, Bull. Torrey Bot. Club 57:616. 1931. TYPE: California: Marin Co.: Vision Hill, W of Tomales Bay, *Eastwood s.n.*, 1 Sep 1900. (HOLOTYPE: CAS!; ISOTYPE: UC!)

Orobanche grayana var. *nelsonii* Munz, Bull. Torrey Bot. Club 57:616. 1931. TYPE: Oregon: Marion Co.: one mile N of Salem, *J. C. Nelson* 2479. (HOLOTYPE: GH!)

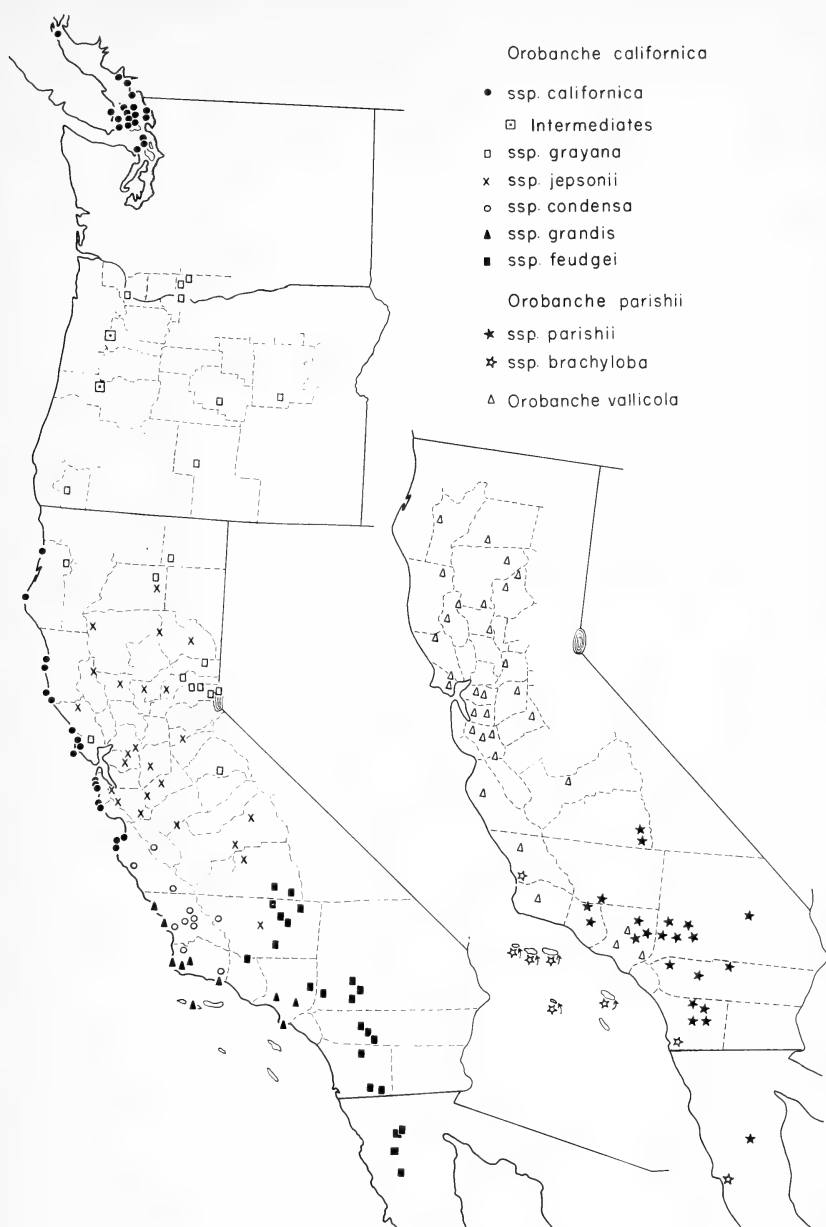


FIG. 5. Distribution of *Orobanchaceae californica*, *O. parishii*, and *O. vallicola* in western Canada, Mexico, and the United States.

Plants 5–20 (27) cm long; stems simple or fastigately branched, the flowers borne in subcorymbose or subcapitate (rarely subspicate) clus-

ters up to 8 cm long; lower pedicels rarely over 1 cm long; calyx lobes 6–15 (20) mm long, usually dark purple; corolla (22) 25–40 (45) mm long, the lobes purplish, sometimes paler externally, the tube fading to whitish or pale yellow; corolla tube conspicuously widening toward throat, the throat 8–10 mm broad; lobes of upper lip oblong-ovate, their apices broadly obtuse (less commonly acute), shallowly retuse, or erosulate; lobes of the lower lip lanceolate to oblong, 8–12 (18) mm long, their apices acute to obtuse; stigma bilamellate with spreading or revolute lobes, occasionally becoming crateriform.

Hosts: Frequently reported on *Grindelia* spp.; also reported on *Erigeron glaucus* in Mendocino Co., Calif. (Daniels, 1 Sep 1965; Roderick, 10 Sep 1961).

DISTRIBUTION: Rare and possibly extinct in meadows of the Willamette Valley, Oregon; occasional on rocky banks and on sandy flats and slopes near the sea in SW British Columbia and in NW Washington on the San Juan Islands and occasionally on the neighboring mainland; occasional in sandy or gravelly soil of coastal bluffs along the California coast from Big Lagoon, Humboldt Co., S to the Monterey Peninsula. Jun–Oct. Known localities (fig. 5):

BRITISH COLUMBIA: Bowen Island, Eagle Cliff, *McBride*, 2 Aug 1964 (UBC); Vancouver, Locarno Park, *Eastham* 5683 (UBC); Mitlenatch Island, Georgia Strait, Fowle, 26 Jun 1961 (V); Vancouver Island, Parksville, *Taylor* 3163 (UBC); Genoa Bay, N side of Cowichan Bay, *Wollaston*, 9 Jun 1927 (V); Saanichton, *Taylor* 3038 (UBC); Oak Bay, Victoria, *Newcombe*, 16 Jun 1924 (WS); Beacon Hill, Victoria, *Macoun*, 14 Jul 1887 (NY, US); South Pender Island, *Szczawinski*, 2 Sep 1955 (UBC, V).

WASHINGTON: SAN JUAN CO.: Sucia Island, *Flett* 2755 (WS); Flat Top Island, *Lawrence* 103 (UC, WS, WTU); Orcas Island, *Eyerdam*, 4 Jul 1935 (UC, UWT); Shaw Island, *Zeller* 890 (NY, US); Wasp Island, *Foster*, 25 Jun 1904 (WS); San Juan Island, Friday Harbor, *Frye*, 25 Jun 1904 (WS). WHATCOM CO.: Lummi Rocks, *Muenschner* 8362 (MO, UC, UTS, WS). SKAGIT CO.: Vandovia Island, *St. John* 7910 (WS); Northwest Island, Deception Pass State Park, *Smith* 1158 (UWT, WS). ISLAND CO.: Whidbey Island, Oak Harbor, *Smith* 1389 (DS). JEFFERSON CO.: Port Townsend, *Otis* 2350 (DS, UC, WS, WTU).

OREGON: [both collections transitional to ssp. *grayana*] MARION CO.: 1 mi N of Salem, *Nelson* 2940 (GH, WS). LANE CO.: Eugene City in 1873 [collector's name not readable] (GH).

CALIFORNIA: HUMBOLDT CO.: Big Lagoon, *Tracy* 6761 (JEPS, UC, UTC); 3 mi S of Cape Mendocino, *Tracy* 4970 (JEPS, UTC). MENDOCINO CO.: Fort Bragg, *Eastwood* 1639 (CAS, GH); Mendocino City, *Daniels*, 1 Sep 1965 (JEPS); 1½ mi SE of Point Arena lighthouse, *Alava*, 5 Oct 1957 (JEPS); ca 1 mi N of Anchor Bay, *Roderick*, 10 Sep 1961 (JEPS). SONOMA CO.: just N of mouth of

Salmon Creek, *Jepson 15950* (JEPS). SAN MATEO CO.: San Pedro, *K. Brandegee* (UC 217609); Farallone City, *Setchell 173* (F, GH, MO, RM, UC); Pillar Point, N end of Half Moon Bay, *Newlon 68* (DAO, JEPS, UC, UTC); near Pebble Beach $1\frac{1}{2}$ mi S of Pescadero Creek, *Hesse*, 30 Jul 1954 (JEPS); Pigeon Point, *Mason 3983* (JEPS, UC, UTC.) MONTEREY CO.: Seaside Station near Monterey, *K. Brandegee* in 1910 (UC); Pacific Grove, *Dudley*, 27 Jun 1905 (DS); S side of Pt. Lobos State Park, *Wilson*, 5 Oct 1937 (UC).

Plants assigned to this subspecies form a fairly discrete and easily recognizable group throughout most of their range. The deep purplish corolla and calyx are unique to these plants in the complex and the maritime habitat common to most of them is shared within their range only by a distinctive undescribed species at San Francisco and southward. The preference of ssp. *californica* for *Grindelia* as a host seems to be a strong one. *Grindelia* is the principal host for only one other subspecies, *O. californica* ssp. *jepsonii* of central California.

Morphological variation within this taxon is only partially correlated with geography. Along the central California coast (Monterey Peninsula north to Pt. Reyes, Marin Co.) the plants mostly have large (35–45 mm long) and broad, deep purple corollas with correspondingly long lips (12–16 mm) and with upper lobes that are broad and rounded at the apex. Munz (1930) referred these plants to *O. grayana* var. *violacea*. There are, however, at the northern and southern extremes of this distribution plants (*Dudley s.n.*, Monterey Co.) that have somewhat smaller (25–35 mm long) and narrower corollas, often with the upper corolla lobes pointed. These plants sometimes have a pale lavender corolla and match quite closely the plants of Humboldt Co. and the Pacific Northwest that were recognized by Munz (1930) as *O. grayana* var. *nelsonii*. This variety was partially sympatric with var. *violacea* and was parasitic on plants belonging to the same host genus. There is no sharp line separating the large-flowered plants from the smaller-flowered ones.

The small-flowered plants of the subspecies are variable in the shape of the stigma and, occasionally, in anther indument. Whereas the stigma of the large-flowered plants is usually bilamellate with thin, spreading, triangular lobes, the stigma in small-flowered plants (Monterey Peninsula, Humboldt Co., and the Pacific Northwest) ranges from small and thin, bilamellate lobes to a thicker, more crateriform type (fig. 4, A). There is no apparent correlation of stigma type with geography. Further complicating construction of identification keys within the *O. californica* group is a variability within this subspecies in density of anther hairs ranging from densely villous (the usual condition) to occasionally nearly glabrous in northern California (*Tracy 6761*, Humboldt Co.).

In the northern distribution of ssp. *californica*, range disjunctions and morphological variants are evident. The plants of the San Juan Islands and vicinity are similar to the small-flowered plants of California in all

respects. Rather similar plants again appear in an inland habitat nearly 320 km distant at Salem, Oregon, growing on *Grindelia*. Judging from herbarium specimens, the corollas are paler and the plants are mostly smaller than the San Juan Island plants, but otherwise the resemblance is close. The Salem plants collected in 1918 and 1919 are the last record in the Willamette Valley region. One would expect the type of *O. comosa* Hook. (a later homonym, renamed *O. grayana* by Beck) collected by David Douglas from the Fort Vancouver area to be similar to the Willamette Valley plants, but only one specimen (fig. 6, D) of four on the holotype sheet (fig. 6, A–D) shows the purplish color of corolla and calyx lobes characteristic of ssp. *californica*. The remaining three plants have a closer resemblance to the reduced, subcorymbose plants with light corollas that occur to the east in mountain meadows (see discussion of ssp. *grayana*). Willamette Valley plants are shown as intermediate between the two subspecies since the plants are mostly smaller and the inflorescence parts somewhat lighter than those of the San Juan Islands (fig. 5).

1b. ***Orobanche californica* ssp. *grayana*** (Beck) Heckard, stat. et comb. nov.

Orobanche grayana G. Beck, Bibl. Bot. 4(19):79. 1890. *Myzorrhiza grayana* (Beck) Rydb., Bull. Torrey Bot. Club 36:695. 1909. Based on: *O. comosa* Hook., Fl. Bor. Am. 2:93. 1838 (not *Orobanche comosa* Wallroth, Sched. Critic. 1:314. 1822). *Anoplanthus comosus* (Hook.) Walp. Repert. Bot. 3:480. 1844. *Phelipaea comosa* (Hook.) A. Gray, Pac. R.R. 4:118. 1857. *Aphyllon comosum* (Hook.) A. Gray, Bot. Calif. 1:584. 1876. TYPE: "Banks of the Columbia, Douglas, Scouler, . . ." (LECTOTYPE: K!; Photograph, UC; see discussion below.)

Plants 4–10 cm in length with short (1–5 cm) stems; inflorescence subcorymbose, few to many-flowered; calyx lobes pallid to occasionally purplish, the lobes (7) 9–13 (16) mm long; corolla (25) 28–33 mm long with widely spreading lips 10–12 mm long, dull white or yellowish to pinkish or pale lavender, often with lavender veins; lower lobes of corolla lanceolate to lance-subulate, pointed, the upper lobes rounded to pointed; stigma thin, bilamellate.

HOSTS: Reported frequently on *Erigeron* and *Aster* and occasionally on grasses.

DISTRIBUTION: Meadows and stream margins, mostly 1,200–1,800 m in California, descending to about 450 m in the Cascade Range of southern Washington; occasionally near sea level. Cascade-Sierra Nevada ranges from Klickitat Co., Wash., S to Tuolumne Co., Calif.; occasionally in the Coast Ranges (S. Oregon and Central California) and mountains of the Columbia Plateau in Oregon. Jun–Oct. Known localities (fig. 5):

WASHINGTON: KLICKITAT CO.: Falcon Valley, *Suksdorf*, 15 Sep 1882 (F, GH, NY, UC, WS); Gilmer, *Suksdorf* 7354 (WS). CLARK

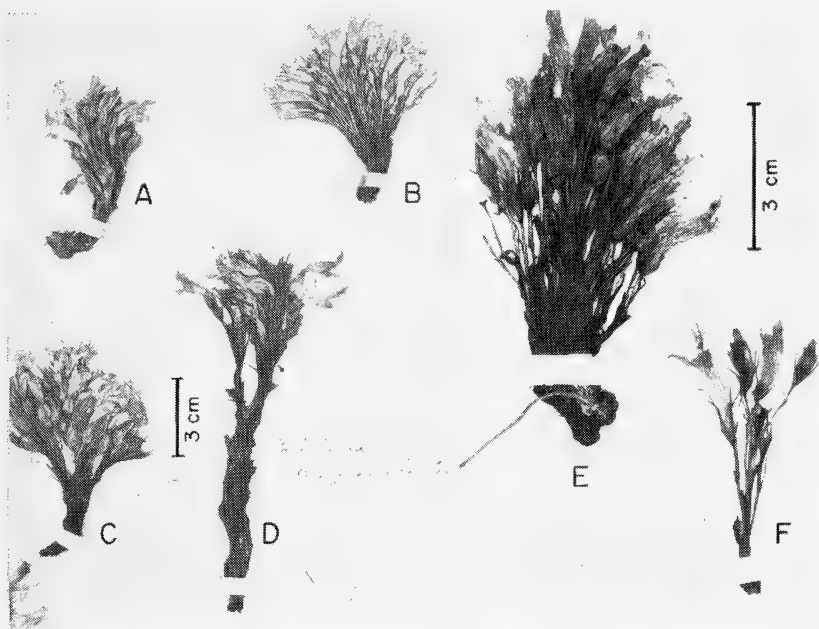


FIG. 6. *Orobanche californica* ssp. *grayana*: A-D, Holotype sheet (Douglas, Scouler) of *O. grayana*. E-F, Douglas collection (presumably No. 386) from vicinity of Fort Vancouver.

CO.: Fort Vancouver, *D. Douglas* 386 (K).

OREGON: HOOD RIVER CO.: Hood River Valley, *Henderson*, 8 Sep 1896 (RM). GRANT CO.: below Pine Spring on N branch of Grasshopper Creek, *Abbott* 3 (WS). CROOK CO.: W of Drake Butte, *Brats* 58 (OSC). LAKE CO.: Summer Lake, *Clark*, Aug 1911 (WILL). JOSEPHINE CO.: lower Illinois River road, *Barnes*, 11 June 1957 (OSC) [atypical in having dark calyx lobes and bracts].

CALIFORNIA: HUMBOLDT CO.: Oregon Creek, Salmon Mts., *Niehaus* 934 (JEPS). MODOC CO.: Egg Lake, *Nutting*, Aug 1915 (UC). SHASTA CO.: Pit River near mouth of Fall River, *Newberry*, 5 Aug 1895 (GH). PLUMAS CO.: Big Meadows, *Austin* in 1879 (SD). SIERRA CO.: Sierra Valley, *Lemmon* in 1874 (JEPS). NEVADA CO.: Loneys Meadow, Bowman Lake area, *Mott*, 22 Sep 1963 (CAS). PLACER CO.: near Summit, *Schreiber* 764 (UC); near Cisco, *Mason* 7177 (UC); Brockway, *Hall & Chandler* 4551 (UC); Tahoe Tavern, Lake Tahoe, *Beans*, 7 Sep 1914 (GH, JEPS). TUOLUMNE CO.: Miguel Meadow, Yosemite National Park, *Mason* 12127 (UC, JEPS). SONOMA CO.: Laguna, Chileno Valley, *Rubtzoff* 6615 (JEPS).

NEVADA: WASHOE CO.: near Reno, *Henning* (NY).

No previous attempt has been made to establish the type specimen and its precise geographic origin for *Orabanche grayana* Beck (based on *O. comosa* Hooker, a later homonym). Hooker's protologue states, "Hab. Banks of the Columbia. Douglas, Dr. Scouler, Dr. Gairdner." Of two possible type sheets (at Kew) collected by David Douglas, one is labeled in Hooker's hand, "Columbia—Douglas, Scouler", and the other is labeled in an unknown hand, "Alluvial grassy plains, Ft. Vancouver". Gairdner's material, which would have been collected in 1833 (McKelvey, 1955), several years after Douglas's, was not represented at Kew. The original drawing of one plant that accompanied the description of *O. comosa* Hook. was pinned to the "Douglas-Scouler" sheet. The drawing best matches the lower left-hand specimen (fig. 6, C) in habit, although the unusual retuse apices of the lower corolla lobes of the original drawing could not be found on any plants of this sheet. Some corollas showing this retuse apex on the lower lobes were found on the Douglas "Ft. Vancouver" collection (fig. 6, E, F), but the two upper lobes were also retuse, a feature not shown in the drawing. I have concluded that the original diagnosis and drawing are composite, not completely accurate for any one specimen, and I have selected the lower left-hand specimen (fig. 6, C) of the "Douglas-Scouler" collection as the lectotype.

The probable collecting locality for the "Douglas-Scouler" specimen can be determined since those two collected together only in April-May and September of 1825 and only in the vicinity of Ft. Vancouver (McKelvey, 1955).

There is a close relationship and intergradation between ssp. *grayana* and ssp. *californica* in the Willamette Valley-Columbia River region of Oregon and southern Washington, and the occurrence of the type collection of *O. grayana* within this region makes identifications critical. Few collections are available and the enormous urban and agricultural developments since the last collection near Salem in 1919 discouraged further search for the plants. The morphological differences of the few available specimens suggest a taxonomic treatment that recognizes the presence of features of both subspecies, mostly those of *grayana* for the Fort Vancouver plants and of *californica* for the collections from Salem and Eugene. The latter clearly show the purple corolla and dark purplish calyx characteristic of ssp. *californica*, although the color appears to be less intense than in the coastal plants. The host for the Salem plants agrees with that of the coastal plants. The collections of Douglas's, on the other hand, largely lack this coloration. Only one plant (from the type sheet, fig. 6, D) has a purple corolla and calyx, and it is also taller (14 cm) than any specimens of ssp. *grayana*. The other specimens of the Douglas collections are short subcorymbose plants with a light calyx and corolla quite like the plants of montane meadows about 100 km eastward in Klickitat Co. (Suksdorf 7354). That the present pallid appearance of the Douglas collections is not a deception due to age is

verified by the excellent description by Douglas (1914) in his published diary for his number 386 from near Fort Vancouver: "flowers white, mixed with rose color, sometimes sulphur-yellow where very much shaded". The sheet (fig. 6, E, F) at Kew labeled "Alluvial grassy plains, Fort Vancouver 1825" is presumably Douglas's number 386 (although it is not so labeled).

The present circumscription of this taxon differs from previous interpretations (Munz, 1930; Ferris, 1960) in that the group is here largely limited to the reduced, montane plants with light-colored corollas (white to pale pinkish, often with lavender veins). My interpretation extends the geographic circumscription beyond these montane plants to include three collections from lowland areas. The first two are David Douglas's collections, including the type of *O. grayana*, that were made west of the Cascade Range in the vicinity of Ft. Vancouver. The montane plants at this latitude are at an elevation of only about 450 m and the presence of the plants farther down the Columbia River at a lower elevation could be explained as a chance establishment of seed from a higher elevation. The other collection from a lowland region is from vernal wet ground in Chileno Valley, Sonoma Co., Calif. (*Rubtzoff 6615*) at an elevation of about 60 m. They were in a region in which ssp. *jepsonii* would have been expected but were considerably smaller and had the corymbose inflorescence of *grayana*. Also, the plants were growing on *Aster*, a genus frequently reported as a host for *grayana* but not for *jepsonii*. Other boreal and montane plants also appear in these cold, marshy areas of the northern California coastal region, including *Menyanthes* (Baker, 1972) and several examples cited by Rubtzoff (1953), who suggests that cooler temperatures brought about by the influence of cool, moist ocean air account for the occurrence of these plants.

Plants of ssp. *grayana* are the most highly reduced plants of the species and, except for the striking difference in habit, are much like those of *jepsonii* of central California, which are postulated to be their nearest relatives. Specimens that appear intermediate are rare but the following occur: Shasta Co., Calif., at 2,800 ft. (*Newberry* in 1855); Butte Co., Calif., at 5,200 ft. (*Copeland*, 13 Sep 1938); Oregon Rogue River at Woodville, (*T. Howell*, 14 Aug 1888, ORE).

1c. *Orobanche californica* ssp. *jepsonii* (Munz) Heckard, stat et comb. nov.

Orobanche grayana var. *jepsonii* Munz, Bull. Torrey Bot. Club 57:617. 1931. TYPE: California: Colusa Co., Princeton, *H. P. Chandler*, Oct 1905 (HOLOTYPE: POM!; ISOTYPE: UC!).

Plants (8) 10–35 cm in length; stems 6–15 cm long below the inflorescence, simple or branched either basally or along the lower half of stem; inflorescence paniculate to racemose, 5–20 cm long; flowers mostly pedicellate, the pedicels decreasing in length upwards in the inflorescence; calyx lobes pallid or pinkish tinged, subulate to linear-subulate,

(8) 10–20 (25) mm long; corolla (25) 30–35 (40) mm long, whitish or pale yellowish brown to pinkish, often with the veins of the lips deep rose or purplish, the tube conspicuously widened toward the throat; corolla lips widely spreading, 10–12 (15) mm long, the lower lobes mostly narrow-lanceolate and pointed, the upper lobes deltoid with acute and often erosulate or emarginate apices; anthers densely villous, 1.5–2.0 mm long; stigma thin, bilamellate with triangular spreading lobes.

HOSTS: *Grindelia* (Brewer 1260, UC; Roderick, 8 Jul 1967; S. Smith 2658; Stinchfield 451), *Baccharis viminea* (Chandler holotype), *Rubus vitifolius* (Jepson 5157), *Chrysothamnus* (Munz 22295).

DISTRIBUTION: Bottomlands and dry hillsides up to 3,000 m. Central Valley and surrounding mountains from the Cascade Range of Shasta and Plumas counties S in the Sierra Nevada to Kern Co.; central California Coast Ranges from Tehama to Santa Cruz counties. May–Oct. Known localities (fig. 5):

CALIFORNIA: SHASTA CO.: Hat Creek, Signal Mt. station, Kramer in 1937 (CAS). PLUMAS CO.: below Mt. Ingalls Lookout, N of Grizzly Valley, 7,800 ft., Balls 15630 (RSA). BUTTE CO.: Jonesville, Copeland, 13 Sep 1938 (UC) [transitional to ssp. *grayana*]. YUBA CO.: Marysville, Bigelow, 25 May 1854 (GH). NEVADA CO.: 1 mi NE of Wolf Mt. (6 mi SW of Grass Valley), Roderick, 8 Jul 1967 (JEPS). COLUSA CO.: Colusa-Williams road, Stinchfield 451 (DS). AMADOR CO.: Pine Grove, Hansen 247 (UC). FRESNO CO.: Kaiser Crest, 9,800 ft., Jepson 13,010 (JEPS); bank of Kings River, 2–3 mi NW of Reedley, Quick 52–350 (CAS); N of Oro Loma, Lyon 570 (UC). TULARE CO.: Visalia, Congdon, Sep 1881 (DS). KERN CO.: 0.5 mi. W of Pyramid Hill, Weston 697 (CAS). TEHAMA CO.: 0.5 mi E of summit of South Yolla Bolly Mt., Tucker & Mann 3554 (DAV). LAKE CO.: Snow Mt., Munz 22295 (RSA). SONOMA CO.: Duncan Mills, M. Jones, 18 Jul 1882 (POM). SOLANO CO.: Haas Slough, N of Rio Vista, Jepson, 8 May 1885 (JEPS). CONTRA COSTA CO.: Antioch, T. Brandegee, Jun 1884 (UC); Mt. Diablo, Elmer 4958 (UC). SAN JOAQUIN CO.: San Joaquin Bridge near Lathrop, T. Brandegee, 9 Sep 1901 (UC). STANISLAUS CO.: 9 mi W of Modesto, S. G. Smith 2658 (JEPS); Cañada del Puerto, near Mt. Oso, Brewer 1273 (GH, UC). SANTA CLARA CO.: Palo Alto, Dudley, 14 Sep 1901 (DS); trail from Madrone Springs to Gilroy Hot Springs, Dudley, 31 May 1895 (DS); Saratoga, Jepson 5157 (JEPS).

The circumscription of this subspecies followed here is similar to that proposed by Munz (as *O. grayana* var. *jepsonii*) except that it has been broadened to include several collections of montane (elevation 1,500 to nearly 3,000 m) plants that heretofore have remained undetermined. These montane plants are sometimes highly reduced (Fresno Co.: Jepson 13,010; Tehama Co.: Tucker & Mann 3554) and thus resemble ssp. *grayana* in size and corymbose inflorescence. They have a more deeply colored corolla (and sometimes calyx) than ssp. *grayana*, how-

ever, and occur in dry, rocky habitats, as do some *jepsonii* of the lower foothills, rather than in moist meadows, as does ssp. *grayana*. Not all these montane plants are reduced and two collections (Shasta So.: *Kramer* in 1937; Plumas Co.: *Balls* 15630) are much like lowlands plants of *jepsonii* in size and habit. There might be some value in creating another subspecies to accommodate these montane plants, but their infrequent and widespread distribution suggests that they are montane variants of *jepsonii* in each region rather than a cohesive genetic entity.

There is intergradation with neighboring subspecies. Thus, some specimens from Santa Clara Co. (as *Dudley*, 31 May 1895) appear to be intermediate towards ssp. *condensa*. Other specimens (*T. Brandegee* in 1884; *Jepson*, 8 May 1885) of the lower delta region of Contra Costa and Solano counties have purple corollas similar to those of ssp. *californica*. Intergradation with ssp. *grayana* is discussed under that subspecies. Identification of ssp. *jepsonii* is complicated by the close relationship to *O. vallicola*, with which it is largely sympatric. This aspect is discussed further under *O. vallicola*.

1d. **Orobanche californica** ssp. **condensa** Heckard, ssp. nov.

TYPE: California: San Luis Obispo Co.: along Yaro Creek, 7½ mi (12 km) N of Pozo, 1,600 ft. (470 m) elevation, *Bacigalupi*, *Ferris*, & *Robbins* 5242, 25 May 1955 (HOLOTYPE: JEPS!; ISOTYPES: NY!, RSA!, US!, WTU!).

Plantae 5–10 (15) cm altae caulibus strictis vel parce fastigiato-ramosis, inflorescentiae pleurumque minus quam 25 floribus subcapitatae vel subcorymbosae; corolla 25–35 mm longa, labii superioris superficie interiore pleurumque rubropurpurata, venis profundius purpureis, labio inferiore albido, purpureotincto, plerumque venis purpureis obsito; corollae faux ca 6 mm lata, tubo lato ad faucem versus parum dilatato; corollae labia 8–10 (12) mm longa, lobis rotundatis vel apice obtusato acutis.

Plants 5–10 (15) cm in length; stems simple or sparingly fastigiate branching, 3–8 (12) cm long, the flowers borne at the top in subcapitate or subcorymbose clusters; calyx 10–16 (20) mm long, the lobes linear-subulate; corolla 25–35 mm long, sordid white to yellowish or brownish externally, the upper lip mostly uniformly reddish-purple on the inner surface with darker purple veins, the lobes of lower lip whitish, purplish tinged, or purple-veined; corolla throat ca 6 mm broad, the tube broad and widening slightly toward throat; corolla lips 8–10 (12) mm long, the lobes of upper lip 2–4 mm long, broadly oblong, their apices obtuse, rounded, rarely acute, often erosulate, or emarginate; lobes of lower lip bluntly acute or obtuse, often retuse or emarginate; stigma bilamellate with triangular lobes.

HOST: *Chrysopsis villosa* (several collections).

DISTRIBUTION: Sandy or gravelly soil, 150–500 m, in California in South Coast Ranges from San Benito to Santa Barbara counties. May–Jul. Known localities (fig. 5):

CALIFORNIA: SAN BENITO CO.: Vancouver Pinnacles, *I. Smith*, 18 Jun 1914 (JEPS). MONTEREY CO.: Tassajara Hot Springs *Elmer* 3240 (DS); W of Bradley, *Hardham* 10781 (RSA). SAN LUIS OBISPO CO.: Cammatti Canyon, 11 mi S of Shandon, *Bacigalupi et al.* 5128 (JEPS); Black Mt., *Hardham* 774 (JEPS); 2 mi S of Huerhuero school, *Lee* 1055 (UC); San Luis Obispo, *Condit*, 7 Jun 1910 (UC). KERN CO.: Temblor Mts., *Hardham* 758 (CAS) [aff. ssp. *feudgei*]. SANTA BARBARA CO.: Blochmans Ranch near Santa Maria, *Eastwood* 479 (CAS); Santa Ynez Mts. toward San Rafael Mts., *H. Ford*, ca 1895 (SBM).

This subspecies accommodates a fairly distinct phase that replaces ssp. *jepsonii* in a region peripheral to the range of the latter. The plants are closest in affinity to those of ssp. *jepsonii* and ssp. *grandis*, differing from them in their smaller stature, in having fewer flowers in a more congested subcorymbose or subcapitate inflorescence, and in having a slightly smaller corolla, often with deeper purplish-red upper lip lobes. A difference in host preference is suggested by the report of only one host, *Chrysopsis villosa*, for 6 collections.

Intergradation of ssp. *condensa* with neighboring subspecies is present. A collection (*Dudley*, DS 10395) from Santa Clara Co. assigned to ssp. *jepsonii* has a short raceme and a large corolla with rather deep reddish purple lips, features that indicate that it is intermediate morphologically between the two subspecies. The plants also occupy an intermediate position geographically. In San Luis Obispo Co. a collection of *Hardham's* (774) has the broader corolla tube reminiscent of ssp. *feudgei* or ssp. *jepsonii*, and another collection (*Hardham* 758) in the Temblor Mts. of Kern Co. is even further removed morphologically from ssp. *condensa* and is an intermediate link, both morphologically and geographically, with ssp. *feudgei*.

G. Thomas Robbins of the Jepson Herbarium first recognized the distinctness of these plants and had proposed a manuscript name that suggested that the plants were confined to or typical of San Luis Obispo Co. Since this subspecies also occurs in several other counties, I have chosen a name that points out the reduction in size of stem, inflorescence, and flower from that of its nearest relatives.

1e. ***Orobanche californica* ssp. *grandis*** Heckard, ssp. nov.

TYPE: California: Santa Barbara Co.: dunes at Surf, *H. M. Pollard*, 22 Jul 1954 (HOLOTYPE: UC!; ISOTYPE: CAS!).

Plantae 8–30 cm altae, caulibus simplicibus vel numerosis fastigiatisque; inflorescentia subcorymbosa, interdum subracemosa; corolla 35–50 mm longa, fauce 9–10 mm lata, gradatim in tubum diam. 4 mm angustata; corollae labiis late oscitantibus, 12–14 mm longis, lobis superioribus latis obtusisque, eis inferioribus lanceolatis vel lanceolato-ovatis, angustatis sed apicis obtusatis.

Plants 8–30 cm long, the stems single or numerous and fasciculate,

(5) 10–20 cm long below the inflorescence, 5–18 mm thick, usually unbranched below; flowers borne in subcorymbose or occasionally subspicate clusters; calyx lobes 15–20 mm long; corolla 35–50 mm long, the tube buff or yellowish with the lips pinkish or pale brownish-red with darker veins (rarely the entire corolla pallid or yellowish); corolla throat 9–10 mm broad, the upper tube tapering to a sinus ca 4 mm in diameter; corolla lips widely spreading, 12–14 mm long, the upper corolla lobes broad and obtuse; lower corolla lobes lanceolate to lance-ovate, acute with blunt apices; stigma bilamellate with triangular lobes.

Hosts: Reported on *Haplopappus venetus* var. *vernonioides* at Surf, Santa Barbara Co. (Pollard in 1954; Carlquist 241, UC), *Adenostoma fasciculatum* (Norris, UCLA), *Artemisia* (Brewer 399), *Heterotheca* (Kimble, 25 May 1961).

DISTRIBUTION: California, sandy soil of dunes, bluffs, and canyons near the coast from San Luis Obispo to Los Angeles counties. Santa Rosa Island. Rare. Apr–Oct (Nov). Known localities (fig. 5):

CALIFORNIA: SAN LUIS OBISPO CO.: ca 1 mi N of Cambria Pines, *H. M. Beard*, 29 Nov 1959 (JEPS); SW end of Morro Bay, *Barnes*, 5 Sep 1960 (SBBG); near Nipomo, *Kimble*, 25 May 1961 (CDA). SANTA BARBARA CO.: head of Mission Canyon, ca 6 mi NE of Lompoc, *Wood*, 20 May 1946 (SBM); Foxin's [Foxen's] Ranch, near Los Alamos, *Brewer 399* (GH); Montecito, *Riedel*, Oct 1928 (SBM); Santa Rosa Island, *Hoffman*, 11 Jun 1930 (SBM). LOS ANGELES CO.: summit of Laurel Canyon road, Santa Monica Mts., *Griesel*, 18 Jun 1936 (LA); Portuguese Bend, *Norris*, 1 Apr 1968 (LA); East Los Angeles, *Abrams*, 13 Jul 1906 (DS) [aff. ssp. *feudgei*].

The plants assigned to this subspecies have been variously identified in the past. The northern coastal specimens from Surf and Cambria were aligned with ssp. *californica*, whereas the southern collections were identified as ssp. *jepsonii* or ssp. *feudgei*. These identifications were due in part to a variation pattern within the subspecies that is partially geographically correlated. The northern populations have purplish corolla lips that are lighter but similar to those of ssp. *californica* of the central California coast and northward. The more southerly populations of ssp. *grandis* have a lighter corolla that is similar to that of ssp. *jepsonii* and a broader corolla that is similar to that of ssp. *feudgei*. None of these variants, however, fits comfortably into these other subspecies, and ssp. *grandis* is proposed to encompass these closely related populations that share a unique combination of features of habit and corolla size and shape.

The closest relationship of ssp. *grandis* is probably with ssp. *californica*, which occupies similar coastal habitats to the north. A gap of 250 km in their known ranges separates the extremes of the two subspecies. The most northern collection assigned to ssp. *grandis* (*Beard*, 29 Nov 1959) is somewhat intermediate between the two subspecies in habit and corolla color. There are no obvious intergrades between ssp. *grandis*

and ssp. *condensa* although their ranges are close. Slight differences in elevation and habitat, and possibly in host preference, separate these subspecies. Likewise, ssp. *feudgei* is apparently separated from ssp. *grandis* by differences in elevation and habitat and host preference. A specimen from East Los Angeles (*Abrams*, 13 Jul 1906), probably collected below 250 m elevation, strongly resembles ssp. *feudgei* and I have identified it as intermediate towards this subspecies.

1f. ***Orobanche californica* ssp. *feudgei*** (Munz) Heckard, comb. et stat. nov.

Orobanche grayana var. *feudgei* Munz, Bull. Torrey Bot. Club 57:616. 1931. TYPE: California: San Bernardino Co.: dry, rocky slope above Baldwin Lake, San Bernardino Mts., 7,500 ft., *Munz 8177* (HOLOTYPE: POM!).

Plants 1–3 dm long, stems (6) 10–18 cm long below the inflorescence, up to 2 cm thick, usually unbranched below, the flowers borne in a subcapitate or subcorymbose cluster, or occasionally in a raceme to 12 cm long; calyx lobes (12) 15–20 (23) mm long; corolla 25–35 mm long, whitish or yellowish to pale rose with darker veins, commonly on drying appearing reddish to brownish red; corolla throat 8–10 mm wide, the upper tube broad and gradually tapering to the sinus; corolla lips (8) 10–12 mm long, the upper corolla lobes broadly oblong and rounded with the apex sometimes emarginate or shallowly retuse, slightly spreading and sometimes reflexed; lower corolla lobes narrowly oblong, subacute or obtuse, sometimes shallowly retuse at apex, usually spreading; stigma bilamellate with triangular lobes.

HOST: *Artemisia tridentata*.

DISTRIBUTION: Washes and open sagebrush flats and slopes. California, from the Kern Plateau of Tulare Co. and the vicinity of Mt. Pinos in Ventura Co. S through the mountains of SW California to the Sierra San Pedro Martir in Baja California; 750–2,500 m. Not common May–Jul. Known localities (fig. 5):

CALIFORNIA: TULARE CO.: S side of Sherman Peak, *Twisselmann & McMillan 14676* (CAS); N end of Long Valley, Kern Plateau, *Howell & True 42817* (CAS). KERN CO.: 5.9 mi E of summit, Greenhorn Mt., *Hardham 2198* (CAS); ridge N of Liepel Peak, Piute Mts., *Breedlove 3874* (CAS, DS); 3.6 mi W of Claraville, Piute Mts., *Breedlove 4010* (CAS, DS); Walker Pass, *Rose*, 10 May 1940 (CAS); top Biss Peak, Tehachapi Mts., *Dudley 393* (DS). VENTURA CO.: Stauffer, Mt. Pinos, *Hall 6327* (UC). LOS ANGELES CO.: Swartout Canyon, San Gabriel Mts., *Abrams & McGregor 654* (DS). SAN BERNARDINO CO.: Lytle Creek canyon, San Antonio Mts., *Hall*, 1–3 Jun 1900 (UC); 37 mi SE of Victorville, San Bernardino Mts., *Holmgren & Reveal 2598* (BRY); S. Fk. Santa Ana River, 6,200 ft., *Grinnell*, 27 Jun 1907 (US). RIVERSIDE CO.: Van Deventer's [Santa Rosa Indian Reserv.], San Jacinto Mts., *Jepson 1458* (JEPS); near Hemet Lake,

Keator, 17 May 1959 (UCSB); S slopes Santa Rosa Mts., *Munz* 5827 (UC). SAN DIEGO CO.: 5½ mi NW of San Luis Rey River Bridge on highway 79, *Weiler & Taylor* 61123 (JEPS); mountains near Jacumba, *Northrup*, 7 May 1935 (UC); Boulevard, *McGregor*, 18 May 1919 (DS).

MEXICO: BAJA CALIFORNIA: near Hanson's Ranch, *Orcutt*, 27 Jul 1883 (UC); 1 mi W of El Rayo, *Moran* 18470 (SD); 1 mi NE of Rancho el Florido, *Moran* 17737 (SD); Aliso, *T. Brandegee*, 30 May 1893 (UC).

The plants with the morphological features defining ssp. *feudgei* correlate fairly well with a distinct ecology and geography. Host records list only *Artemisia tridentata*, and the geographical area occupied by ssp. *feudgei* coincides rather well with the southwestern range of that *Artemisia* (Ward, 1953).

Some morphological variation is worth noting. The most striking is an atypical corolla that has a narrower sinus of the lower tube and an upper flaring tube with narrower and more pointed lower lobes, all features of ssp. *jepsonii*, rather than the characteristic broad tube of ssp. *feudgei*. These variants, however, have the typical habit of ssp. *feudgei* and are scattered throughout the range of this subspecies (Kern Co.: *Breedlove* 3874; San Diego Co.: *Northrup* in 1935). In addition, the host for one of the collections (*Breedlove* 3874) is noted as *Artemisia tridentata*.

There appears to be some intergradation of ssp. *feudgei* with those subspecies with juxtaposing ranges, i.e., ssp. *grandis* and *condensa*, as discussed under those subspecies. There is no evidence of intergradation with *O. vallicola* of lower elevations.

The most intriguing relationship of ssp. *feudgei* is that to *O. corymbosa* (Rydb.) Ferris, which appears to be a reduced version of ssp. *feudgei* with the same host preference. Collins (1973) has pointed out the usefulness of placentation for *Orobancha* taxonomy and the arrangement of the placenta can be used to distinguish the two taxa: *O. corymbosa* has two parietal placentae per ovary while in ssp. *feudgei* (and all of *O. californica*) each of these two placental areas is separated into two distinct placentae, thus forming four placentae per ovary. This feature shows up well either in the ovary or in the dehiscent carpel. Corolla color also seems to be a consistent difference between the two taxa with *feudgei* having a much lighter corolla than *corymbosa*, in which the corolla lips are a deeper purplish or maroon. Where the ranges of the two species approach each other (southern Sierra Nevada, Tulare Co., and Piute Mts., Kern Co.), there is no definite evidence of intergradation. Variant specimens of ssp. *feudgei* are present in the Piute Mts. but are not clearly intermediate between the two species. One specimen (*Twisselmann* 7358, JEPS) has a corolla that is more similar in size and shape to that of other subspecies of *O. californica* in its narrower lip lobes and widely flaring lips. The other specimen (*Smith* 864, JEPS), unfortunately a fasciated

one, has a corolla like that of *corymbosa* but with the habit and size more like *feudgei*.

2. ***Orobanche vallicola*** (Jepson) Heckard, stat. et comb. nov.

O. comosa var. *vallicola* Jepson, Man. Fl. Pl. Calif. 952. 1925. TYPE: California: Santa Clara Co.: river bottom, Coyote, *Jepson 6196* (HOLOTYPE: JEPS!; ISOTYPE: GH!, MO!).

O. californica var. *claremontensis* Munz, Bull. Torrey Bot. Club 57: 618. 1931. TYPE: California: Los Angeles Co.: Claremont, *D. L. Crawford 574*, 8 Jul 1916. (HOLOTYPE: POM!; ISOTYPES: DS!, UC!).

Plants single-stemmed or sparingly branched at base, 7–40 cm long, the underground stem below the inflorescence 5–30 cm long and up to 20 mm in diameter; scales broad and obtuse on lower stem, narrowing upwards on stem and becoming narrow-triangular to subulate as bracts in the inflorescence; inflorescence subspicate or racemose, occasionally paniculate, 4–30 cm long, glandular-puberulent throughout; lower pedicels 5–25 mm long, usually decreasing in length upwards, bearing opposite subulate bracts 5–10 mm long; calyx lobes narrow-subulate, often with the apex attenuate, (6) 9–15 (20) mm long, pale or pinkish tinged, the tips sometimes revolute; corolla 17–28 (30) mm long, whitish or yellowish to pinkish tinged, often with the veins of lips and upper tube darker pink or purplish, the palatal folds yellow; corolla lips usually widely spreading, 5–9 (10) mm long, the upper corolla lobes triangular or triangular-ovate with acute and pointed apex; lower corolla lobes narrow-triangular to lanceolate with acute apex; anthers ca 1.5 mm long, glabrous or villous in varying degrees along the dehiscent margins; stigma bilamellate with strongly downward curving lobes or somewhat peltate-crateriform with margins rolled downward; capsule ovoid to cylindric-ovoid, 10–13 mm long; seed ovoid, ca 0.5 mm long.

Hosts: Frequently reported to be parasitic on *Sambucus*. Also reported on pear [*Pyrus*] (*Chandler*, Oct 1905), *Quercus agrifolia* (*Crawford 547*), *Symphoricarpos albus* (*Linsdale 259*), *Baccharis douglasii* (*Jepson 6196*).

DISTRIBUTION: Woodlands, thickets, and openings, lowland valleys and foothills; occasional in widely scattered localities, cismontane California from Trinity Co. S to Los Angeles Co. Rare. May–Nov (as early as Mar in S. Calif). Known localities (fig. 5):

CALIFORNIA: TRINITY CO.: Hyampum, *Blasdale*, 11 Jun 1896 (UC). SHASTA CO.: Anderson, *Rich*, Nov 1921 (DS). TEHAMA CO.: S rim of Mill Creek Canyon *Quick 49–47* (CAS). BUTTE CO.: Chico, *E. Copeland*, 2 Nov 1936 (UC). COLUSA CO.: Princeton, *Chandler*, Oct 1905 (UC); Sycamore Slough, *Stinchfield*, 12 Jul 1916 (DS). SACRAMENTO CO.: Sacramento, *Savage*, 11 Jun 1964 (CDA). MENDOCINO CO.: Covelo, *Murphey*, 16 Oct 1946 (OSC). LAKE CO.: Kelsey Creek, ca 2 mi S of Kelseyville, *Schulthess*, 13 July 1931 (UC). SONOMA CO.: Russian River near Cloverdale, *Lile*, 1 Oct 1933 (UC,

JEPS). MARIN CO.: Novato, *Kessel*, 16 Sep 1956 (JEPS); San Anselmo Canyon, *Sutcliffe*, Oct 1924 (CAS). ALAMEDA CO.: Centerville, *Gammon*, Aug 1955 (CDA); near Livermore, *Hammond*, Aug 1896 (JEPS). CONTRA COSTA CO.: Russellmann Park, N base of Mt. Diablo, *R. Smith*, 23 Sep 1956 (JEPS); Marsh Creek road, 3 mi above Clayton, *Mason* 5432 (JEPS). SAN JOAQUIN CO.: Mokelumne River, Lodi, *Switzenberg*, 13 Jul 1964 (CDA). STANISLAUS CO.: Tuolumne River bottom, Empire, *E. Morse*, 10 Jun 1939 (JEPS). SANTA CLARA CO.: Mt. Hamilton, *R. Smith* 10 (UC); Saratoga, *Fablinger*, Oct 1894 (UC). MONTEREY CO.: Hastings Reservation, Santa Lucia Mts., *Linsdale* 259 (CAS); Redwoods, Santa Lucia Mts., *Palmer* 338 (F, GH, MO, UC, US). SAN BENITO CO.: Zanger Ranch, Pacheco Pass highway, *Dermody*, 18 Aug 1965 (CDA). SAN LUIS OBISPO CO.: Atascadero, *Huffman*, 11 Nov 1964 (OBI). FRESNO CO.: San Joaquin River bottom, N of Fresno, *Quibell* 2084 (RSA). SANTA BARBARA CO.: Figueroa Mt., *Hoffman*, 7 Jun 1929 (SBM). LOS ANGELES CO.: Tick Canyon, *MacFadden* 16187 (CAS); Santa Monica Canyon, *Barber*, 3 Jul 1898 (UC); Claremont, *Harwood* 3275 (POM).

This species has essentially the same circumscription as the combined concepts of *O. californica* vars. *californica* and *claremontensis* in Munz (1930). Munz's var. *claremontensis*, a local variant from the Claremont region of eastern Los Angeles Co., was distinguished by a deeply cut upper lip of the corolla. I have examined another collection (*Harwood* 3275) from this locality with corollas less deeply cut (about $\frac{1}{2}$ the lip length) than those of the type collection, indicating that this feature is a variable one in this region and does not in itself justify varietal rank for the plants.

A baffling relationship of this species, as well as one that gives difficulty in identification, is that with *O. californica* ssp. *jepsonii*. The separation of these two largely sympatric taxa (fig. 5) is sometimes difficult owing to the variability of their diagnostic features. The two taxa are distinguished by a combination of characters, no one of which is absolute, at least as seen in herbarium materials, and any of the characters can be variable and intergrading between the two species. Thus *vallicola* typically has a stem that is more thickened basally and that becomes darker on drying; the inflorescence is subspicate with only the lowermost flowers having pedicels, in contrast to the racemose or paniculate inflorescence of ssp. *jepsonii* with longer pedicels nearly throughout; similarly the calyx lobes are usually shorter in *vallicola*. The corolla of *vallicola* is typically smaller, the lips shorter with narrower, more pointed lobes; the anthers are slightly smaller than those of ssp. *jepsonii* and are either glabrous or at least less villous, with the hairs largely confined to the region of dehiscence. Perhaps the most consistent feature of *vallicola* is a stigma in which the lobes are decurved apically (fig. 4, J-L) and often laterally, thus becoming crateriform (fig. 4, L) in contrast to the spreading, laminate, and triangular lobes of the stigmas of ssp. *jepsonii*.

(fig. 4, F). Data on hand suggest a difference in host preference with *vallicola* usually parasitic on trees or occasionally shrubs, whereas ssp. *jepsonii* is usually reported on *Grindelia* or other herbaceous perennials of the Compositae. The report of the type specimen of *O. californica* ssp. *jepsonii* on the shrub *Baccharis viminea* is an exception.

Recognition of the *vallicola* plants as a species apart from *O. californica* ssp. *jepsonii* follows previous workers (Beck, 1930; Munz, 1931; Ferris, 1960), who also recognized and commented on the close affinity of the two. In spite of the overlap in diagnostic features separating these two largely sympatric groups, two recognizable forms emerge that seem adequately distinct for recognition as separate species.

3. *Orobanche parishii* (Jepson) Heckard, comb. et stat. nov.

Orobanche californica var. *parishii* Jepson, Man. Fl. Pl. Calif. 952. 1925. TYPE: California: San Bernardino Co.: Bear Valley, San Bernardino Mts., S. B. Parish in 1894 (HOLOTYPE: JEPS!).

Plants single-stemmed or sparingly branched at base, the stems 5–26 cm in length and up to 15 mm in diameter, simple or occasionally branched above; scales broadly ovate becoming (as bracts) lance-ovate or broadly triangular in the inflorescence, multi-veined with more than 5 conspicuous parallel veins; inflorescence subspicate, usually densely glandular-puberulent throughout, the flowers mostly sessile with the lowermost occasionally on short pedicels rarely over 1–2 cm long; bractlets opposite, subulate, less than 10 mm long; calyx lobes subulate to subulate-attenuate, 6–18 mm long, pallid or pinkish to purplish tinged; corolla 15–25 mm long, curving outward in older flowers, whitish or yellowish to buff, the lips buff to pinkish with maroon veins or tinged with purplish-red, moderately to sparsely glandular externally; corolla lips 4–8 mm long, erect to spreading or recurved, the upper lip cleft 2–3 mm into 2 oblong or oblong-ovate lobes with rounded to truncate and often retuse or erosulate apices; lower lobes of corolla narrower, rounded or blunt at tip, often retuse or erosulate; palatal folds of the tube well developed; anthers 1.5–2.0 mm long, glabrous or moderately villous along the dehiscent margins; stigma bilobed, often unequally so, the triangular or rounded lobes thin or thick, spreading to recurving; capsule oblong-ovoid, 7–10 mm long; seed brown, irregularly ovoid, favose-reticulate, ca 0.4–0.5 mm long.

HOST: Various shrubs and herbaceous perennials; apparently different for the two subspecies, q.v.

DISTRIBUTION: Southern California and northern Baja California. Rare (fig. 5).

In elevation of *O. californica* var. *parishii* to a species, the prevailing concept of the group as one of montane Southern California is expanded not only to include plants of the surrounding lowland areas but also to add a new subspecies to accommodate related plants of the California Channel Islands and coastal mainland.

The plants are rare and information on habitat and hosts, flower color, and chromosome number is scanty. Only two chromosome counts are available (Chuang & Heckard, in prep.), a count of $n = 24$ for ssp. *parishii* and one of $n = 48$ for ssp. *brachyloba*.

KEY TO SUBSPECIES OF *O. PARISHII*

- Corolla 2.0–2.5 cm long with corolla lips 6–8 mm long; calyx lobes subulate-attenuate, mostly 10 mm or longer; anthers hairy or occasionally glabrous; stigma lobes thin, spreading but not recurving; mostly montane, Southern California ssp. *parishii*
- Corolla 1.5–2.0 cm long with lips 4–6 mm long; calyx lobes subulate, usually less than 10 mm long; anthers glabrous; stigma lobes thick and usually recurving outwardly; California Channel Islands, rare on coastal mainland ssp. *brachyloba*

3a. *OROBANCHE PARISHII* (Jeps.) Heckard ssp. *PARISHII*

Stem simple, 15–22 (10–26) cm long; inflorescence 5–8 (3–14) cm long and 2.5–4.0 cm broad, narrow and moderately dense; calyx-lobes 10–13 (6–18) mm long, the tips often recurving; corolla 18–25 mm long, often sharply curved at nearly a right angle to the axis in older flowers, yellowish or lavender-tinged with darker veins, in dried specimens the lips brownish or buff with 3 conspicuous maroon veins; upper lips spreading or recurved, lower lips spreading; anthers moderately villous along the dehiscent margins, occasionally glabrous; stigma bilobed, often unequally so, funnellform, the lobes thin, spreading

HOST: Reported to be mostly parasitic on shrubs: *Adenostoma* (Perrison 416), *Arctostaphylos* (Fosberg, 12 Aug 1931), *Eriodictyon* (Johnston 1762). Also reported on *Corethrogyne filaginifolia* (Wallace 562).

DISTRIBUTION: Open chaparral or scrub, 600–2,100 m (rarely 150–2,700 m) elevation. Mountains of cismontane Southern California: Kern Plateau, Tulare Co., and Mt. Pinos, Ventura Co., S to the Sierra San Pedro Martir of Baja California. Rare in the Mohave Desert. Mar–Sep (Nov). Known localities (fig. 5):

CALIFORNIA: TULARE CO.: Kennedy Meadows, Kern Plateau, Howell & True 43822 (CAS); N end of Lamont Meadow, Howell & True 43758 (CAS). VENTURA CO.: Iris Point, Mt. Pinos, Heckard & Chuang 2732 (JEPS); Topatopa Mts., Red Reef Canyon, Abrams & McGregor 127 (DS). KERN CO.: Old Fort Tejon, Tehachapi Mts., Hall 6301 (UC), Coville & Funston 1159 (US) [both specimens aff. *O. vallicola*—see text]. SAN BERNARDINO CO.: Mohave Desert, Victor, Wright, June 1888 (UC); Old Dad Mt., Cottonwood Spring, M. Jones, 14 May 1926 (POM); San Bernardino Mts., above Lake Arrowhead, Clokey 5308 (UC); San Antonio Mts., Devils Backbone, Johnston 1762 (UC). LOS ANGELES CO.: San Gabriel Mts., Mt. Islip summit, Fosberg & Ewan 792 (LAM); San Gabriel Mts., Arraster Creek, Pierson 416 (JEPS); N of River Reservoir, Davidson, Aug 1889

(LAM); Santa Anita Canyon, *Moxley*, 1 Sep 1913 (LAM). RIVERSIDE CO: San Jacinto Mt., *Hoffman*, 8 Sep 1929 (SBM); Joshua Tree National Monument, Smith Water Canyon, *Schenk* (RSA); Box Springs Mt., near Riverside, *Wallace* 562 (POM). SAN DIEGO CO.: Warner Hot Spring Mt., Eagle Nest, *Gander* 286 (SD); Julian, *T. Brandegee*, 12 Jun 1894 (UC); Ramona, *T. Brandegee*, 29 May 1894 (UC).

BAJA CALIFORNIA: La Encantada, Sierra San Pedro Martir, *Wiggins* 16623 (DS).

Removal of plants of ssp. *parishii* from their taxonomic alignment as a variety of *O. californica* (= *O. vallicola* in this treatment) is based on the consistent differences in corolla and bract between the two groups and on their sympatric association in the Los Angeles basin without their loss of identity. The bract (fig. 3, L–N) is broader than in *O. vallicola* and has a larger number (over five) of parallel veins and the corolla has broader lobes that are obtuse and rounded at the apex rather than acute and pointed. There are also differences in corolla color and texture in the dried specimens, the corolla of ssp. *parishii* being buff-colored (off-white to yellowish in *O. vallicola*) often with reddish-brown lobes and veins (purplish in *O. vallicola*). In texture the corolla of ssp. *parishii* is thicker and less brittle. It seems likely that these corolla features will be even more pronounced in fresh material.

Two specimens that appear to be intermediate between ssp. *parishii* and *O. vallicola* have been collected near Fort Tejon in Kern Co. The earlier collection (*Coville & Funston* 1159) in 1891 shows a greater resemblance to *O. vallicola* than does the collection of 1905 (*Hall* 6301). This later collection, however, possesses the long, narrow, pointed lower lobes of the corolla that is typical of *O. vallicola*.

3b. *Orobanche parishii* ssp. *brachyloba* Heckard, ssp. nov.

TYPE: CALIFORNIA: Ventura Co.: Dutch Harbor, San Nicolas Island, *Raven & Thompson* 20794 (HOLOTYPE: JEPS; ISOTYPES: DS, RSA).

Plantae 5–18 cm altae; inflorescentia subspicata, crebra, 3–10 (15) cm longa; calycis lobi 7–9 (11) mm longi; corolla 15–24 mm longa, demum sursum vel horizontaliter curvata, plerumque glandulosissima, fulva, plerumque violaceotincta; corollae labia 4–7 mm longa, antherae glabrae (raro glabrescentes); stigma bilobata, lobis eius crassis decurvatis.

Plants with 1 stem or several from branching base; stem simple or occasionally with a few secondary branches from the midpoint or below, 5–18 cm long; inflorescence subspicate, dense, 3–10 (15) cm long; calyx lobes 7–9 (11) mm long, subulate; corollas 15–24 mm long, directed upwards or curving outward in age, usually abundantly glandular, buff to yellowish, often tinged along veins of lips with purplish-red; corolla lips 4–7 mm long, erect or slightly spreading; anthers glabrous (rarely sparsely villous); stigma bilobed, the lobes usually thick and

strongly decurving, sometimes crateriform.

HOST: Mostly reported to be growing on *Haplopappus* (usually *H. venetus*); *Atriplex californica* (Philbrick B65-1526) and *Eriogonum latifolium* (Benedict, 10 Sep 1967) also are suspected hosts.

DISTRIBUTION: Sandy soil near beaches. Santa Barbara Channel Islands and San Nicolas and Santa Catalina islands of California; occasionally on the mainland in San Luis Obispo and San Diego counties and in Baja California. May-Sep. Known localities (fig. 5):

CALIFORNIA: SAN LUIS OBISPO CO.: dunes S of Oso Flaco Lake, Hoover 10870 (OBI). SANTA BARBARA CO.: San Miguel Island: Cuyler Harbor, Blakley 5875 (JEPS), Harris Point peninsula, Philbrick B65-1526 (SBBG); Santa Rosa Island: W end, Hoffman, 9 Aug 1930 (CAS, SBM); Santa Cruz Island: S end of Christi Beach, Benedict, 10 Sep 1967 (SBBG). VENTURA CO.: San Nicolas Island: Jackson Hill road to beach (W side), 700 ft, Blakley 4157 (SBBG). LOS ANGELES CO.: Santa Catalina Island: Ben Weston Beach, Thorne & Everett 34392 (JEPS, RSA, SBBG). SAN DIEGO CO.: Silver Strand, Purer 2923 (SD).

BAJA CALIFORNIA: El Rosario, T. Brandege, 20 May 1889 (F).

Plants of this largely insular subspecies differ from those of ssp. *parishii*, a mainland and largely montane group, in several minor features that in their total effect present two easily recognizable entities. Variation of these features within each subspecies, however, results in an overlap in these definitive characters that makes it difficult to formulate a key that allows decisive identification in all cases. These differences consist of an overall decrease in size in ssp. *brachyloba*: the stems and inflorescence are shorter, the corolla and calyx-lobes are shorter. In addition, ssp. *brachyloba* has shorter corolla lips that are erect or only slightly spreading rather than recurved and their color, at least in pressed specimens, is a purplish-red tinge throughout while ssp. *parishii* has buff or yellowish lips with conspicuous maroon veins. The corollas of ssp. *brachyloba* are not as conspicuously curved outward in older flowers as in ssp. *parishii*. Glabrous anthers and a very dense spike are the usual condition for *brachyloba*, whereas the anthers of ssp. *parishii* are more often hairy and the flowers of the spike are less crowded. Although sporadic variation may occur in any of these features, the overall difference between the two groups warrants their taxonomic recognition. One variant deserves special mention: The only collection from Santa Catalina Island (Thorne & Everett 34392) approaches ssp. *parishii* in almost all the above features. Because of its similarity in habitat and geography with ssp. *brachyloba*, however, I am assigning this collection to that taxon.

There are some differences among the collections from different islands, probably reflecting the independent evolution of the isolated populations. Plants from San Nicolas Island (Raven & Thompson 20794) in general possess the most distinctive features in comparison

to ssp. *parishii*. Plants from the northern islands along the Santa Barbara Channel are fairly similar but have more pointed corolla lobes.

Three collections from the coastal mainland seem more similar to the island plants than to the montane plants of ssp. *parishii*. One, a collection from San Luis Obispo Co. (Hoover 10870), is unusual in having anthers that are sparsely hairy and lower corolla lobes that are broader than usual.

The only other species of the *O. californica* complex that has been collected from the Channel Islands is *O. californica* ssp. *grandis*, on Santa Rosa Island (Hoffman, SBM).

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ANOTHER LOOK AT LEIBERGIA COULT. & ROSE
(UMBELLIFERAE)

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Among the extensive gatherings made in northwest America in the 1840's by the observant, Dresden-born botanical explorer Charles A. Geyer was a small umbelliferous plant that has remained obscure to this day. William J. Hooker (1847) described it under the collector's manuscript name *Peucedanum* (*Ferula*) *tenuissimum*, and provided a brief description of the vegetative parts and flowers since no fruit was available. The type collection, *Geyer 302*, was made "in wet swampy small prairies surrounded by lofty mountains, Coeur d'Alene country", growing with *Thlaspi* (Cruciferae). In their monograph of 1900, Coulter and Rose remarked that the plant was "... still doubtful. It is probably a good species, but more than likely has been described under some other name" (p. 240). Mathias (1937) placed it in synonymy under *Lomatium ambiguum* (Nutt.) Coult. & Rose but without comment and without seeing authentic material.

Coulter and Rose relied on collections of a small, bulbous umbelliferous plant from the Coeur d'Alene Mountains and the Spokane area of eastern Washington as the basis for erecting the genus *Leibergia* in 1896. They compared this plant both to certain tuberous species of *Peucedanum* (= *Lomatium*) and to *Orogenia*, but stressed its technical affinity with *Oreomyrrhis* and *Chaerophyllum*, presumably because of the elongated, wingless, and laterally compressed fruit. In his lengthy critique of the Coulter and Rose (1900) treatment of *Lomatium*, Marcus E. Jones (1908) substituted *Cogswellia* as a generic name and transferred all the species from one genus to the other in sectional groups. The fifth, section *Cous*, was characterized as possessing tuberous roots, narrow leaf divisions, and narrow fruit wings. Among the yellow-flowered species — actually the petals are white, the anthers yellow — was also included *Cogswellia* (*Leibergia*) *orogenioides*. Mathias (1937) followed Jones' interpretation of this species but returned it to the restored *Lomatium*. In the general geographical area only that genus was known to contain bulbous forms, although the absence of lateral (marginal) fruit ribs was atypical.

In 1943 we described *Tauschia hooveri* from the Yakima region, a species markedly similar to *Leibergia orogenioides* and almost certainly congeneric with it. (Compare the illustrations: Madroño 7: 66, fig. 1. 1943 and Contr. U. S. Nat. Herb. 3: pl. 27. 1896.) However, it did not occur to us at the time to make comparison with any species of *Lomati-*

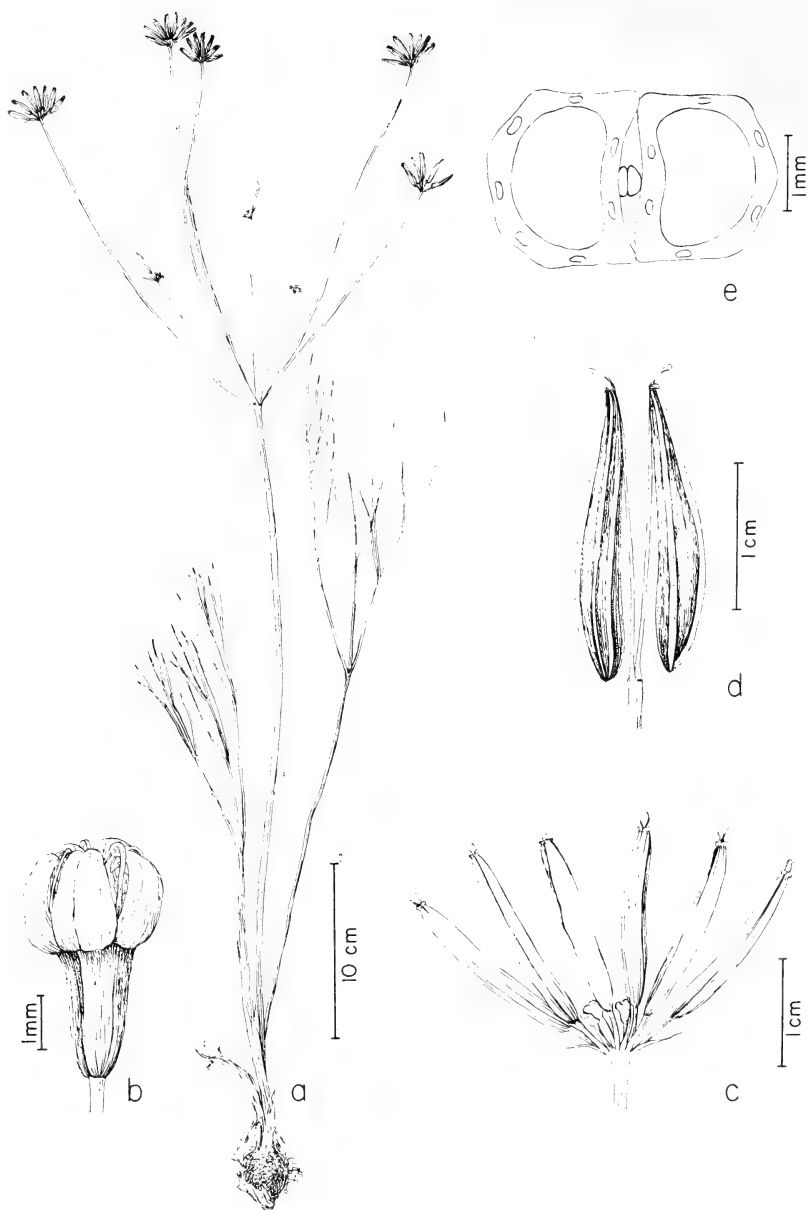


FIG. 1. *Tauschia tenuissima*: a, habit; b, fertile flower; c, fruiting umbellet; d, fruit; e, fruit transection. (a, c-d from Meyer 901; b, from Suksdorf 8645; e, from Leiberg 1027)

um. Twenty years later, Constance examined the Geyer collections in the British Museum, at Kew, and in Vienna, and discovered that *Peucedanum tenuissimum* Hook. is unquestionably the same thing as *Leibergia orogenioides* Coult. & Rose. This taxon, moreover, is very much closer to *Tauschia hooveri* than it is to any species of *Lomatium*, and should no longer be separated from it generically.

There are three possible ways of bringing these related taxa together. The first is to refer them both to *Lomatium*, where they would join a number of species of very similar appearance occurring in the same general region. However, the low bulbous habit, which occurs not only in *Lomatium* and *Orogenia*, but also in such diverse genera as *Bunium*, *Scaligeria*, *Diposis* (*Hydrocotyloideae*), and *Sanicula* (*Saniculoideae*), is a poor guide to relationship. So long as considerations of fruit morphology continue to dominate classification of Umbelliferae, it is inconsistent to admit the laterally lightly compressed fruits of these two species to the same genus with the dorsally flattened and usually marginally winged ones of *Lomatium*. The second alternative, to revive the genus *Leibergia* and to assign the two related taxa to it, is perhaps the most attractive. The two species are very similar in appearance and not very far separated geographically, and there are no other species of *Tauschia* as close to either one of them as they are to each other. When one searches for solid distinctions to set off *Leibergia* generically from *Tauschia*, however, it seems clear that a third alternative is unavoidable, that is to transfer *Leibergia orogenioides* to the genus *Tauschia* as:

Tauschia tenuissima (Geyer ex Hook.) Math. & Const., comb. nov., (fig. 1).

Peucedanum tenuissimum Geyer; Hooker, London Journ. Bot. 6:235. 1847.

Leibergia orogenioides Coult. & Rose, Contr. U. S. Nat. Herb. 3:575. 1896.; *Cogswellia orogenioides* M. E. Jones, Contr. West. Bot. 12:33. 1908; *Lomatium orogenioides* Mathias, Ann. Mo. Bot. Gard. 25:242. 1937.

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UTRICULARIA (LENTIBULARIACEAE) IN THE PACIFIC NORTHWEST

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Three species of *Utricularia*, i.e. *U. vulgaris* L., *U. intermedia* Hayne and *U. minor* L., have been reported from Oregon, Washington, and British Columbia (Piper 1906, Ferris 1950, Cronquist 1959, Peck 1961, Steward et al. 1960, Taylor 1966). Henry (1915) reported an additional species, *U. occidentalis* A. Gray, which was later mentioned by Ferris (1950) in a short note and by Cronquist (1959) as a synonym of *U. minor*. *Utricularia ochroleuca* R. Hartm. was reported from British Columbia by Porsild (1951) and by Boivin (1966).

In 1970 and 1971, we noticed that *Utricularia gibba* L. was common in several lakes in the vicinity of Victoria, British Columbia. Several specimens of *U. gibba* in British Columbia herbaria (V, UBC, UVIC; the last abbreviation used for the herbarium of the University of Victoria) had been misidentified as *U. minor*. This fact together with the uncertain relation of *U. occidentalis* to *U. minor* led us to this revision of *Utricularia* in the Pacific Northwest.

The present study is based on examination of *Utricularia* in the following herbaria: DAO, CAN, CAS, JEPS, POM, OSC, RSA, UBC, UC, UVIC, V, WS, and WTU. Species descriptions are based on herbarium material from the study area. Notes on the ecology of *Utricularia* species are the result of field observations made primarily on Vancouver Island.

KEY TO UTRICULARIA IN THE PACIFIC NORTHWEST

Leaf margin and winter buds setose.

Leaves pinnatifid, with more than 20 terete ultimate segments, usually with numerous bladders *U. vulgaris*

Leaves dichotomously divided, with fewer than 20 flat ultimate segments, usually without bladders.

Spur of flower more than $\frac{1}{2}$ the length of the lower lip, cylindrical, positioned at an acute angle to the lower lip; tip of the leaf segments obtuse, with an abruptly starting bristle, the ultimate segment usually with more than 3 bristles on each side arising from the leaf margin *U. intermedia*

Spur of flowers less than $\frac{1}{2}$ the length of the lower lip, pyramidal, positioned at a right angle to the lower lip; tip of leaf segments acute, gradually narrowed to a bristle, the ultimate segment usually with less than 4 bristles on each side arising from small teeth on the leaf margin. *U. ochroleuca*

Leaf margin and winter buds glabrous.

Leaves with more than 5 ultimate segments, these flattened and gradually narrowed toward the tip; inflorescence of 3–9 flowers; bracts auriculate; upper lip of corolla less than $\frac{1}{2}$ the length of the lower lip, spur less than $\frac{1}{2}$ the length of the lower lip; pedicels recurved in fruit; seeds not winged. *U. minor*

Leaves with fewer than 5 ultimate segments, these filiform; inflorescence of 1–3 flowers; bracts not auriculate; upper lip of corolla equalling the lower lip, spur almost as long as the lower lip; pedicels not recurved in fruit; seeds winged. *U. gibba*

UTRICULARIA VULGARIS L., Sp. Pl. 18. 1753. (figs. 1; 2)

Utricularia macrorhiza Le Conte, Ann. Lyceum Nat. Hist. New York 1:73. 1824.

Utricularia vulgaris L. subsp. *macrorhiza* (Le Conte) Clausen, Cornell Univ. Agric. Exp. Sta. Mem. 291:9. 1949.

Utricularia vulgaris L. var. *americana* A. Gray, Man. Bot. ed. 5:318. 1867.

Aquatic herb with stolons 20–180 cm long. Leaves pinnatifid, 2–9 cm long, divided into 20–150 filiform segments. Bladders attached near the base of the points of branching in leaves on stalks 0.1–1.0 mm long. Bladders on primary branches larger than those of the others, 1.0–4.0 mm long and 0.5–4.0 mm wide, 10–50 per leaf, sometimes lacking on one of the stolon branches. Winter buds 7.0–30 mm long, 6–15 mm wide, setose. Scape 10–30 (40) cm tall with 1–5 bract-like scales. Inflorescence of 3–15 bright yellow flowers. Pedicels 6–30 mm long, recurved after anthesis, bracts 2.5–8.0 mm long. Calyx lobes subequal, 3–6 mm long and 2–4 mm wide, the lower one emarginate. Upper lip of corolla ca 10 mm long (3–17 mm), the lower lip 12 mm long (5–20 mm), approximately equal in length and breadth. Spur 10 mm long, hook-like, slightly shorter than the lower lip. Fruit a globose capsule ca 6 mm in diameter. Palate gibbous, as large as the upper lip, sometimes with reddish brown veins.

Utricularia vulgaris, *U. intermedia* and *U. minor* belong to a circum-polar boreal species group with a gap in the distribution of *U. intermedia* and *U. vulgaris* in Iceland and of *U. vulgaris* also in Greenland. The range of *Utricularia minor* has small discontinuities in Asia and America (Hultén 1937, 1968, 1971).

Utricularia vulgaris is widely distributed from British Columbia to California. It grows in a variety of habitats ranging from lower sublittoral to littoral zones in lakes and ponds of diverse trophic levels. It is common in stands of *Brasenia schreberi* Gmel., *Potamogeton natans* L., *Scirpus validus* Vahl. In shallower water it occurs with *Sparganium minimum* L. and *Scirpus subterminalis* Torr. It grows in stands of *Nuphar polysepalum* Engelm. and in successional stages with *N. polysepalum*, *Carex lasiocarpa* Ehrh., and *Menyanthes trifoliata* L.

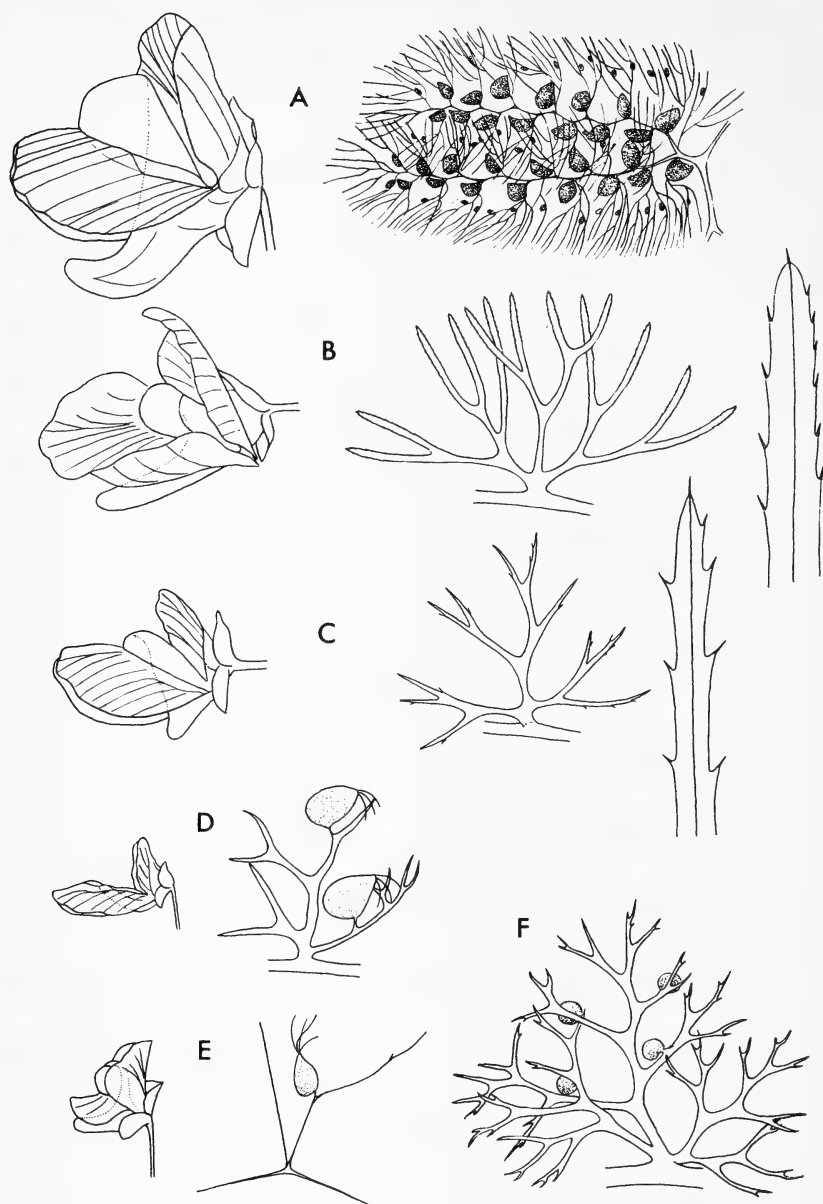


FIG. 1. *Utricularia vulgaris* (A), *U. intermedia* (B), *U. ochroleuca* (C), *U. minor* (D), *U. gibba* (E), leaf of the robust form of *U. minor* (F). Orig. O. Ceska.

The American populations of *Utricularia vulgaris* have been differentiated from the European *U. vulgaris* at the level of species (Britton and Brown 1913, Hultén 1949), subspecies (Hultén 1968) or variety (Fasset 1940, Porsild 1951). The crucial distinguishing character of American plants is the narrower and longer spur. DeCandolle (1844) was unable to distinguish American specimens of this species from those in Europe. Rossbach (1939) and Fernald (1941) considered the two to be conspecific. This conclusion was accepted by several workers (Merrill 1948, Taylor 1964, Calder and Taylor 1968). Fernald's treatment apparently was based mainly on published descriptions of the European *U. vulgaris*. The description of *Utricularia vulgaris* has often been confused with the description of the closely related *Utricularia neglecta* Lehm. (Casper 1967). Furthermore, Fernald (1941) used Hegi's illustration of "*Utricularia vulgaris*" (Hegi 1914, Tafel 244, Fig. 5c), which Glück (1936) and Casper (1967) claim is in fact *Utricularia neglecta*. Recently Taylor (1971) has equated *U. neglecta* with *U. australis* R.Br., the latter name having priority. The confusion existing in the *Utricularia vulgaris* complex can only be resolved by a comprehensive study of all members (including the Japanese species) throughout their distribution.

UTRICULARIA INTERMEDIA Hayne, J. Bot. (Schrader) 1800 (1):18. 1800. (figs. 1; 2)

Aquatic or semi-terrestrial herb with aquatic leafy stolons lacking bladders and subterranean leafless stolons with bladders. Leafy stolons 10–50 cm long. Leaves 5–30 mm long, divided in three parts and then dichotomously divided into 6–20 ultimate segments that are flat with a central nerve, blunt obtuse tip, and abruptly starting bristle. Ultimate segments usually with 2–10 short bristles on each side from the leaf margin. Bladders 1.5–4.5 mm long and 1.0–3.0 mm wide; their stalks usually without branches, ca 0.5–4.0 mm long. Winter buds 2–15 mm long and 3–10 mm thick, setose. Scape 5–20 cm tall with 1 or 2 bract-like scales. Inflorescence of 3–5 bright yellow flowers. Pedicels 3–15 mm long, ca 4 times the length of their corresponding 1.5–4.0 mm long bracts. Calyx lobes subequal, 2.5–3.5 mm long and 2.0–3.0 mm wide. Upper corolla lip ca 6.5 mm long (4–9 mm), lower lip 12 mm long (5.5–18 mm) and ca 15 mm wide (7–20 mm). The spur cylindrical, straight, 8–12 mm long, positioned at an acute angle to the lower lip. Palate ca 7 mm long. Fruit a capsule ca 3 mm in diameter.

Utricularia intermedia is scattered in British Columbia and is considerably rarer in Washington. Herbarium specimens examined included no record from Oregon. *Utricularia intermedia* occurs in oligotrophic and dystrophic lakes and in marshes. It is commonly associated with *Carex lasiocarpa*. In the sublittoral zone it grows in mats anchored in mud. Occasionally it grows in stands of *Nuphar polysepalum* and *Scirpus subterminalis* together with *Utricularia vulgaris* and *Utricularia minor*.

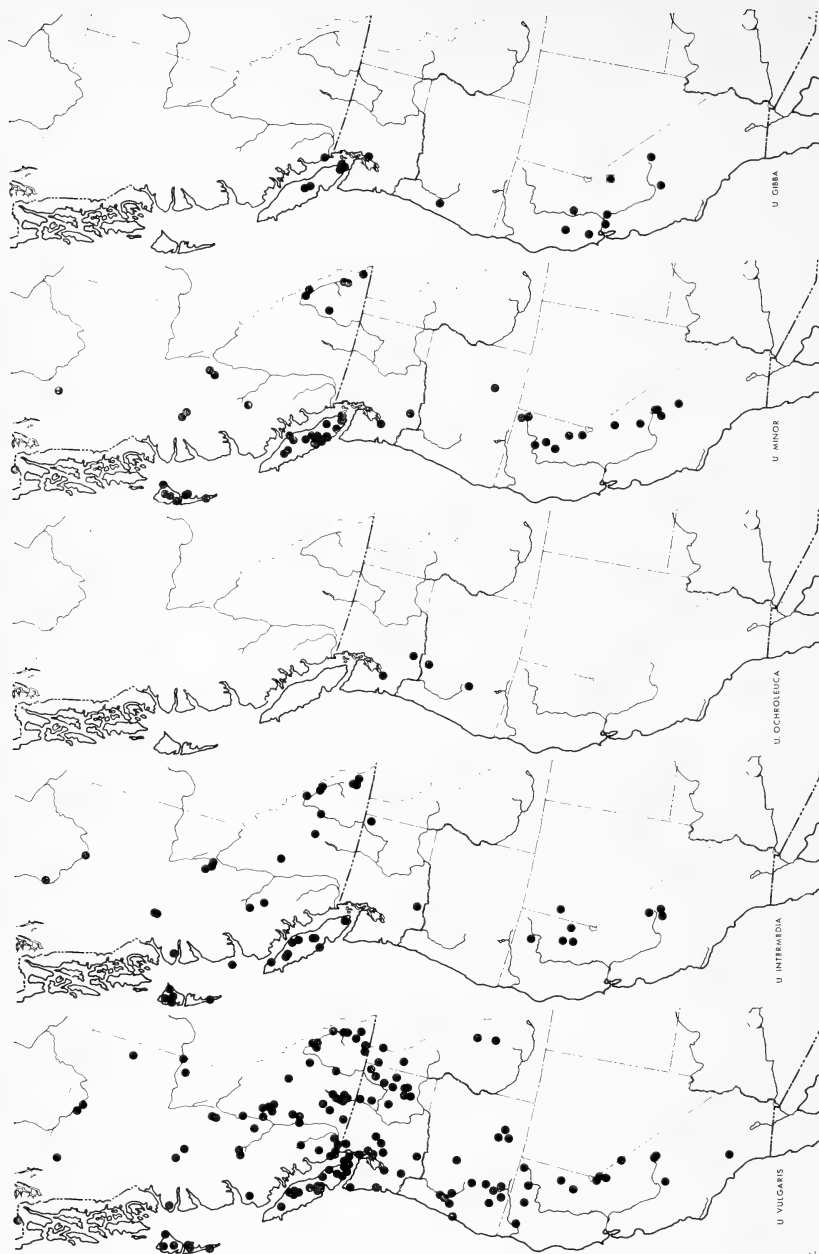


FIG. 2. Distribution of *Utricularia vulgaris*, *U. intermedia*, *U. ochroleuca*, *U. minor*, and *U. gibba* in the Pacific Northwest and California.

In the Pacific Northwest, *Utricularia intermedia* is quite uniform in morphology. There is a slight variation in vegetative organs related to the depth of water in which the plants grow.

UTRICULARIA OCHROLEUCA R. Hartman, Bot. Not. 1857:30. 1857 (figs. 1; 2)

Utricularia occidentalis A. Gray, Proc. Amer. Acad. Arts 19:95. 1883.

Aquatic or semi-terrestrial herb with stolons 5–30 cm long, differentiated into leafy aquatic and leafless subterranean stolons. Leaves 3–15 mm long, divided into 3 parts that are dichotomously divided into 5–19 ultimate segments. These with a central nerve and gradually narrowed into a bristle. The ultimate segment usually with 1–4 hairs on each side, arising from small teeth on the leaf margin. Leaves occasionally bear one bladder. Bladders developed on leafless stolons, smaller than in *U. intermedia*, about 1.5–2.5 mm long and 1.0–2.0 mm wide. Winter buds 1.5–4.0 mm long, 1.2–2.5 mm thick, with setose segments. Scape 5–25 cm tall with 1–5 bract-like scales. Inflorescence of 2–10 lemon-yellow flowers. Pedicels 2–15 mm long, straight in anthesis but slightly recurved after, ca 4 times longer than auriculate bracts. Calyx lobes subequal, ca 2.5–3.5 mm long, 1.5–2.0 mm wide, lower lobe emarginate. Upper lip of corolla 4.5 mm long (3–9 mm), lower about 8.5 mm long (5–12 mm) and a little narrower. Spur pyramidal with broad base, 3.0–4.0–5.5 mm long, positioned at a right angle to the lower lip. Palate 5 mm long.

The distribution of *U. ochroleuca* is very poorly known. Sterile specimens are difficult to distinguish from those of *U. intermedia* with which it can be easily confused.

Utricularia ochroleuca is distinctive when in flower. The characteristic pyramidal spur, 3.0–5.5 mm long, positioned at a right angle to the lower lip, differs from that of all other species of *Utricularia* in the region. In the sterile stage *U. ochroleuca* is easily distinguished from *U. minor* because of the glabrous leaves of the latter. It is less easily distinguished from *U. intermedia* by having hairs arising from teeth on the leaf margin, acute tips on the leaf segments, and fewer hairs on each side of the final leaf segments. Other characters that have been suggested to differentiate *Utricularia ochroleuca* from related species include the possession of acute winter bud segments (Glück 1902, 1913, 1936, Hegi 1914) and bladder stalks leafy on the subterranean stolons (Fernald 1950). However, these characters are not reliable. Sporadic occurrence of bladders on normal leaves of leafy stolons of *U. ochroleuca* differentiate this species from *U. intermedia*, a species that rarely has bladders on its leaves.

In Europe, *Utricularia ochroleuca* is rare, known only from northern, central, and western parts. Walter and Straka (1970) listed *U. ochroleuca* among the European subatlantic geoelements with a footnote "also in Eastern North America". In North America, the distribution of *U.*

ochroleuca is wider than indicated in floristic works. According to Porsild (1943), the first record of *U. ochroleuca* from North America west of Greenland was that by Perry (1931) from St. Paul Island, Nova Scotia. Boivin (1966) reported this species from the continental Northwest Territories, Alaska, Greenland and Nova Scotia, from Quebec to Manitoba, and in British Columbia.

Boivin's report of *Utricularia ochroleuca* from British Columbia seems to be based on that of Porsild (1951), who collected a specimen of a sterile *Utricularia* from Liard Hot Springs (CAN 99616, *A. E. Porsild*, June 2, 1944). This sheet of specimens was identified by Porsild as *U. ochroleuca*, an identification confirmed by Boivin's annotation. A later re-examination of this sheet by Porsild led to the "+ *U. intermedia* Hayne". In our opinion, all specimens on this sheet are *U. intermedia*. So far we have seen no specimen of *U. ochroleuca* from British Columbia.

The first collection of *Utricularia ochroleuca* in the Pacific Northwest and, apparently, the first collection of this species in North America was made by W. N. Suksdorf in Falcon Valley, Klickitat Co., Washington in 1880. Based on Suksdorf's specimens collected in 1880 and 1883, Gray (l.c.) described a new species—*Utricularia occidentalis*. All of Suksdorf's specimens of *U. occidentalis* that we have examined belong to *U. ochroleuca*, a species not known from North America in Gray's time.

Utricularia occidentalis has been treated in different ways. Henry (1915) reported it from Ucluelet, Vancouver Island, based on Macoun's report (Macoun 1913). Macoun's specimen (CAN 99609)—identified as "*Utricularia minor* L. or *Utricularia occidentalis* A. Gray"—is a robust form of *U. minor*. Ferris (1950) mentioned *U. occidentalis* in a short note under *U. minor* as, "An imperfectly known species which differs from *U. minor* by the hairy-fringed leaf-segments of the winter buds." Cronquist (1959) noted *U. occidentalis* as a synonym of *U. minor* with the comment, "A form with both the spur and the palate a little better developed than usual." Consequently the illustration of *Utricularia minor* in Cronquist (1959) is in fact one of *Utricularia ochroleuca*. Rossbach (1939) mentioned both *U. ochroleuca* and *U. occidentalis*. He regarded the latter as, "seemingly endemic . . ." [to] ". . . the region of Falcon Valley, in western Klickitat Co., Washington." He implied that *U. occidentalis* may be a hybrid between *U. intermedia* and *U. minor*. Other authors (Böcher et al. 1968, Boivin 1966) have suggested a similar hybrid origin for *U. ochroleuca*. Whether the latter is a good species or a hybrid remains a matter for conjecture.

In the herbarium material studied, we found several specimens of *Utricularia ochroleuca* misidentified either as *U. minor* or as *U. intermedia*. In Washington it has been collected in Falcon Valley, Klickitat Co., by Suksdorf in 1880, 1882, 1885, 1923, (WS, WTU, CAN, CAS), and somewhere near Olympia by Kincaid in 1896 (one plant on the herbarium sheet WS 24589 with *U. minor*). *Utricularia ochroleuca* was

collected in Oregon on Mt. Hood by Thompson in 1927 (WS) and in Gold Lake, Lane Co., by Ingram in 1926 and by Dennis in 1962 and 1963 (OSC). We have found one collection of *U. ochroleuca* from Colorado (Chalk Creek, 17 mi N of Salida, Chaffee Co., 7500 ft., *Hitchcock, Rethke* and *Raadshooven* 1938, CAS), and one from Illinois (Sunny Spring Bog, 3 mi. N of East Peoria, Tazewell Co., *Chase* 11938, 1951, WS).

UTRICULARIA MINOR L., Sp. Pl. 18. 1753. (figs. 1; 2)

Aquatic or semi-terrestrial herb with stolons 15–75 cm long differentiated into aquatic stolons with leaves and subterranean stolons with fewer leaves and more bladders. Leaves 2–10 mm long, dichotomously divided into 2–17 ultimate segments. Ultimate segments acute to acuminate, lacking a central nerve. Small, leathery, brown-tinged, deeply divided remnants of winter buds often found on the stem. Bladders 1.5–2.0 mm long and 0.7–1.5 mm wide, 2–6 on each leaf. Winter buds globose 2–4 mm in diameter, glabrous. Scape 5–15 cm tall with 1–4 bract-like, purple scales. Inflorescence of 2–10 pale yellow flowers, the two lower flowers sometimes approximated. Pedicels 2–10 mm long, recurved after anthesis. Bracts purple, 1–2 mm long, auriculate. Calyx lobes equal, 0.5–2.5 mm long, 0.5–2.5 mm wide, lower lobes emarginate. Upper lip of corolla 2–4 mm long, shorter than lower lip, 5.0–7.5 mm long and 4.0–4.5 mm wide. Spur small, saccate, 1–2 mm long. Palate low, ca 3–5 mm long. Fruit a globose capsule ca 2.0–2.5 mm in diameter.

Utricularia minor is less common than *U. intermedia*. Extensive collecting in some areas (e.g. Queen Charlotte Islands and Vancouver Island) suggests that it is frequently overlooked because of its smaller size. *Utricularia minor* grows in oligotrophic and dystrophic lakes and in peatbog pools. We have found it growing with *Sparganium minimum* and *Scirpus subterminalis* in shallow muddy water, in stands of *Menthanthes trifoliata*, and in peatbog pools with *Sphagnum* spp. and *Lycopodium inundatum* L.

A robust form of *Utricularia minor* has been collected on several occasions in British Columbia. Its stolons are ca 50–120 cm long with internodes ca 3–10 mm long. Leaves are 9–20 mm long, orbiculate and divided into 20–40 final segments (fig. 1, F).

UTRICULARIA GIBBA L., Sp. Pl. 18. 1753. (figs. 1; 2)

Aquatic or semi-terrestrial herbs with 10–25 cm long filiform stolons, often characteristically zig-zag shaped in floating stolons. Leaves 3–10 mm long, filiform, dichotomously branched from the base, one branch usually straight, and without bladders, the other usually branched, with 1–3 bladders. Bladders 0.5–1.5 mm long, 0.5–1.0 mm wide, with long branched hairs at the membrane opening. Bladders progressively reduced to small protuberances toward the ends of leaves. Winter buds absent. Scape 3–7 cm tall, with one or no scale. Inflorescence of 1–2

bright yellow flowers. Pedicels straight after anthesis, 5–10 mm long. Bracts semi-amplexicaulous, not auriculate. Calyx lobes equal, orbiculate, 1.5–2.5 mm long. Upper lip of corolla 2–6 mm long, flat, positioned at a right angle to the lower lip. Lower lip 3.5–6.0 mm long, slightly wider than long. Spur 3–5 mm long, cylindrical, straight, positioned parallel to the lower lip. Palate conspicuous, 3.0–4.5 mm long. Fruit a 2-valved capsule ca 5 mm in diameter, seeds lenticular, winged.

The distribution of *Utricularia gibba* is entirely different from that of the other *Utricularia* species in the region. It and other closely related species occur mainly in Central and South America and Africa. Of related species, only *U. exolata* R. Br. (Portugal: Glück 1936) and *U. biflora* Lam. (Hungary: Soó 1968) grow in Europe in isolated localities. Taylor (1964) referred to *Utricularia gibba* as the most widely distributed *Utricularia* species: pantropically occurring, "almost throughout the New World from NE United States to Argentina and in Africa from Nigeria (apparently absent from Madagascar)." It grows from eastern North America westward to Oklahoma, Minnesota, and Michigan (Fernald 1950) and in Canada in Ontario, Quebec, New Brunswick, and Nova Scotia (Boivin 1966).

In the Pacific states *Utricularia gibba* was first recorded in California by Mason (1931) who listed several localities that were mentioned again in Rossbach's (1939) treatment. In British Columbia it is common in several lakes near Victoria (Blinkhorn, Florence, Glenn, Prior, Teanook, and Thetis) in Ash, Patterson, and Turtle Lake near Port Alberni and in Beaver Lake in Vancouver. In Washington, *U. gibba* was collected by Piper from Mud Lake, Seattle in 1892 (WTU) and misidentified as *U. minor* (cf. Piper 1906). In Oregon it was collected in Long Tom River S of the Monroe Bridge by Dennis in 1969.

In the vicinity of Victoria, *Utricularia gibba* grows with *Brasenia schreberi*, *Utricularia vulgaris*, and *Ceratophyllum demersum* L. We have not seen floating material in flower. *Utricularia gibba* often flowers while growing with *Sphagnum* in stands of *Dulichium arundinaceum* (L.) Britt. or on muddy soil in disturbed places. Near Port Alberni *U. gibba* occurs attached to the lake bottom in *Carex lasiocarpa* stands or on steep submerged banks that are overgrown with *Rhynchospora alba* (L.) Vahl and *Drosera anglica* Huds. *Utricularia gibba* grows here in water 10–70 cm deep. Some plants have differentiated leafy aquatic and leafless subterranean stolons.

The long cylindrical spur, broad lower lip, and the upper lip equalling the lower lip easily distinguish *U. gibba* from *U. minor*. The identification of sterile specimens is more difficult. Rossbach (1940) states, "Though the most reduced leaves [of *U. minor*] resemble those of *U. gibba*, they still are usually coarse and not quite like those of *gibba* in appearance, and their comparatively large bladders are less darkly colored and much more, in fact nearly quite, homogeneous in size." *Utricularia gibba* can be recognized by the presence of rudimentary

bladders on the leaves. Leaves of *U. gibba* are usually divided from the base into two opposite parts.

Utricularia gibba belongs to a complex of several species, including *U. fibrosa* Walt., and *U. biflora* Lam., that becomes more intricate in Central and South America (Rossbach 1939). Some authors (see Taylor 1964) treat *U. fibrosa* and *U. biflora* as mere synonyms of *U. gibba*. However, we circumscribe *U. gibba* in the restricted sense.

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NOTES AND NEWS

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ESTUARINE MACRO-ALGAE OF YAQUINA BAY, NEWPORT, OREGON

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Previous taxonomic and ecological investigations of the macro-algae of the Pacific Coast have been primarily descriptive of the algae of the open coast. The estuarine algae have been omitted or treated only incidentally. As a result, our knowledge of the algal species of the open coast is much more complete than our understanding of the algal flora of estuaries. The coastal marine algal flora of Oregon has been investigated by a number of phycologists and was summarized by Sanborn and Doty (1944) and Doty (1947a and 1947b). The present study was undertaken in conjunction with a study of the salinity and temperature tolerances of some macro-algae of Yaquina Bay (Kjeldsen and Phinney, in press.)

Yaquina Bay is located on the central Oregon Coast and drains approximately 389 square km of the central Coast Range. Free tidal access is provided by the maintenance of twin jetties at the mouth of the estuary resulting in a strong marine influence extending approximately 15 km into the estuary. The widest point (3.2 km) of the estuary is near the mouth; above this point the estuary gradually narrows into the Yaquina River.

The collecting stations established in the bay correspond to the reference navigational markers (fig. 1). The stations were sampled monthly over a two year period, from January 1964 to January 1966. Specimens were sampled either by SCUBA diving or during low tides. The specimens were returned to the laboratory for identification and many of these were mounted for a permanent record. Duplicates have been deposited in the herbarium of the Oregon State Marine Science Center and in the collections of the authors.

SPECIES PRESENT AND THEIR HABITATS

The zones of vertical distribution of algae listed are in accordance with those given in most phycological literature. The intertidal zone lies between high water and low water of the extreme spring tides. The sublittoral zone extends downward from the low water of the extreme low tides. Algae in the upper and mid-intertidal zones are usually exposed during low tides; those in the lower intertidal are only exposed occasionally; and those in the subtidal are never exposed. Depths in



FIG. 1. Map of the survey area showing collecting stations. Numbers 1-6 are "spurs" or groins on the south jetty. Numbers 7-47 refer to reference navigational markers.

meters are determined from the mean low tide. The species present in Yaquina Bay, their habitat, tidal zone, temperature, and salinity ranges, are presented in Table I.

TEMPERATURE AND SALINITY TOLERANCE

Data concerning the temperature and salinity regimes in the estuary (Kjeldsen and Phinney, in press) have been used together with collection data for the algal inhabitants to determine their distribution with relation to temperature and salinity. The results showed that the majority of the species are found in 33 to 30 ‰ salinity and of these 75 were red algae, 28 brown algae, and 23 green algae. Analysis of the temperature data showed that the majority of the species were found in 10-12° C; of these 73 were red algae, 29 brown algae, and 24 green algae. Only six species were found in salinities ranging from 33 to 5 ‰, and only 15 species were found in temperatures ranging from 20 to 10° C; all other species had narrower tolerance ranges.

DISTRIBUTION OF SPECIES AND SEASONAL OCCURRENCE

Approximately 90 per cent of the species of algae of Yaquina Bay and estuary are found in the area from the end of the jetties at the mouth of the estuary to the Yaquina Bay bridge. Most algae in this area are characteristic of the open coast and may be considered "invaders". A few taxa, such as *Ulva expansa*, *Laminaria saccharina*, *Sargassum muticum*, and *Gracilaria sjoestedtii*, are found only in areas such as this. From the Yaquina Bay bridge to Marker 21, there is a transition zone containing both marine and brackish water algae.

The distribution of some species may be limited by the lack of suitable substrate. Most benthic plants require a firm surface for attachment, and the substrate must be free of silt for sporelings to develop. In the estuary available substrates include large boulders on a shifting, sandy bottom at the north and south jetties, a sandstone reef with tidepools between the north jetty and Yaquina Bay bridge, rock rubble of the fills along the estuary, and mud with some cobble and other debris from Marker 15 to Elk City. Shells, pilings, logs, and dock floats also provide common substrates. The log floats of docks along the estuary constitute a unique habitat, as the organisms colonizing them in the spring are never exposed by the tides, but always remain near the surface where the light intensity is high and the problem of siltation is relatively minor. The general effect is of a sub-tidal habitat. Algae are absent, with a few exceptions, in the lower intertidal zone along the main channel from Marker 15 to the Toledo bridge, probably because of lack of suitable substrate, constant exposure to currents, and the presence of moving silt. A rather lush vegetation of *Fucus*, *Enteromorpha*, *Chaetomorpha*, *Gracilaria*, and *Ulvaria* occurs, however, in protected locations in side channels and sloughs in this area.

Perennating vegetative structures were observed in a number of forms during the winter. The encrusting basal disks of *Heterochordaria*, *Petalonia*, and *Corallina*, were common on the jetty during December, January, and February and resumed growth in the spring. Species of *Iridaea* and *Gigartina* persisted over the winter as basal holdfasts and resumed growth in the spring. *Laminaria saccharina* on the floats of the port docks died back to the stipe and resumed growth in the spring in competition with young germlings. *Laminaria setchellii* and *L. sinclairii* showed similar responses. The holdfast and basal portions of the stipe of *Egregia* persisted through the winter, often in a battered and highly epiphytized state, resuming growth in the spring. *Sargassum* died back to its holdfast and a few basal branches and resumed growth in the spring. The greatest changes occurred in the upper and middle intertidal zone. Most of the algae were eaten or decayed back to their holdfasts during winter. Many other species, particularly some of the red algae in the lower intertidal and subtidal, were not markedly affected by winter conditions and continued growth and reproduction throughout the year.

In Yaquina Bay and estuary three seasonal vegetations can be distinguished: 1) spring; 2) summer; and 3) fall and winter. The largest number of species and the greatest production of biomass occur during the spring and summer. From November to February the biomass is greatly diminished by peak occurrence of epiphytes and animal grazers, winter storms, silt, low salinities, and short photoperiod. There is however, a distinctive winter flora. Judging from direct visual observation there appear to be two periods of decline and decay, one of the spring vegetation in the early summer, and another of the summer vegetation

in the fall. Evidence of this is seen in the windrows of debris that accumulate on the shores.

A very diverse algal vegetation exists in Yaquina Bay, yet some of the species common on the rocky outer coast of Oregon that are conspicuously lacking in Yaquina Bay include the following: *Codium setchellii* Gardner, *Codium fragile* (Suring) Hariot, *Ralfsia* spp., *Coilodesme californica* (Ruprecht) Kjellman, *Desmarestia* spp. with one exception, *Pleurophycus gardneri* Setchell & Saunders, *Costaria costata* (Turner) Saunders, *Macrocystis integrifolia* Bory, *Lessoniopsis littoralis* (Farlow & Setchell) Reinke, *Postelsia palmaeformis* Ruprecht, *Pterygophora californica* Ruprecht, *Cystoseira osmundacea* (Menzies) C. Agardh, the coralline algae with three exceptions, *Plocamium violaceum* Farlow, *Farlowia mollis* (Harvey & Bailey) Farlow & Setchell, *Ahnfeltia plicata* (Hudson) Fries, and *Stenogramme californica* Harvey. *Macrocystis integrifolia* Bory was found on several occasions in large floating mats. These had entered the bay from offshore.

Among the algae collected in the Yaquina estuary the following are new records for Oregon: *Chaetomorpha aerea*, *Phaeostrophion irregulare*, *Haplospongidion gelatinosum*, *Halymenia californica*, *Gracilaria verrucosa*, *Porphyra smithii*, and *Neodilsea americana*.

The authors are indebted to Dr. Isabella Abbott for her identification of *Neodilsea* and verification of *Halymenia* and *Schizymenia*.

TABLE 1. SPATIAL DISTRIBUTION, SEASONAL OCCURRENCE, SALINITY AND TEMPERATURE RANGES OF MACRO-ALGAE IN YAQUINA BAY. Collection locations and reference navigational markers are shown in Figure 1. Salinity data are expressed in parts per thousand (‰) and temperature in degrees centigrade.

Chlorophyta

- Blidingia marginata* (J. Agardh) Dangard. Growing on *Salicornia* (pickle grass) of mud flats or in tide pools in the upper intertidal; Summer; markers 15 to 37; 33–15 ‰; 20–13° C.
- Bryopsis corticulans* Setchell in Collins, Holden & Setchell. On rocks or logs in the lower intertidal to a depth of 3 m in subtidal; Spring, Summer, and Fall; 6th Spur to marker 21; 33–25 ‰; 20–10° C.
- Cladophora gracilis* (Griffiths) Kützinger. On mud flats, rocks, or logs in the middle intertidal; Spring; 1st Spur to marker 25; 33–20 ‰; 16–10° C.
- Cladophora trichotoma* (C. Agardh) Kützinger. On rocks in the upper intertidal; Spring, Summer, Fall and Winter; 6th Spur to 3rd Spur; 33–30 ‰; 16–10° C.
- Enteromorpha clathrata* (Roth) Greville. On rocks, logs, epiphytic, or free floating in the middle to lower intertidal; Spring, Summer, Fall and Winter; 6th Spur to Toledo Bridge >33–5 ‰; >20–13° C.
- Enteromorpha compressa* (L.) Greville. On rocks and logs in the upper intertidal; Summer, Fall and Winter; 1st Spur to marker 47; 33–20 ‰; 20–10° C.
- Enteromorpha intestinalis* (L.) f. *clavata* J. Agardh. On rocks, shells, logs, or epiphytic on *Fucus* in the upper intertidal. In January, February, and March, a distinct and obvious green zone of this species appears on the rocks of the estuary in what would correspond to an extreme high intertidal or splash zone; Spring, Summer, Fall and Winter; 3rd Spur to Toledo Bridge; >33–>5 ‰; >20–>10° C.

- Enteromorpha intestinalis* (L.) Link f. *cylindricea* J. Agardh. This may simply be a growth form of f. *clavata*. Free floating; Spring and Summer; 3rd Spur to marker; 30–5 ‰; 20–10° C.
- Enteromorpha linza* (L.) J. Agardh. On rocks, shells, or logs in the lower intertidal to mid-intertidal; Spring, Summer, Fall and Winter; 6th Spur to marker 37; >33–25 ‰; 20–10° C.
- Enteromorpha tubulosa* Kützting. On logs or rocks in the upper intertidal; Summer and Fall; 3rd Spur to Toledo Bridge; 30–10 ‰; 20–<10° C.
- Enteromorpha angusta* (Setchell & Gardner) Doty. On rocks, logs or epiphytic in the lower intertidal to a depth of 3 m; Spring, Summer, Fall and Winter; 6th Spur to marker 37; >33–30 ‰; 16–<10° C.
- Kornmannia zostericola* (Tilden) Bliding. Epiphytic on *Zostera* in the lower intertidal; Summer and Fall; North Jetty flat to marker 15; 33–30 ‰; 12–10° C.
- Rhizoclonium riparium* (Roth) Harvey. On rocks, mud, logs, or entangled on other algae in the lower intertidal; Spring, Fall and Winter; markers 12 to 47; 33–10 ‰; 16–10° C.
- Spongomorpha coalita* (Ruprecht) Collins. On rocks, logs, or epiphytic in the lower intertidal; Spring, Summer and Fall; 6th Spur to Port Docks; 33–25 ‰; 12–10° C.
- Spongomorpha spinescens* Kützting. Epiphytic in the lower intertidal; Spring, 6th Spur to North Jetty flat; 32–28 ‰; 12–10° C.
- Ulothrix implexa* Kützting. On rocks in the upper intertidal zone; Spring; 6th Spur only; 33–30 ‰; 12–10° C.
- Ulva expansa* (Setchell) Setchell & Gardner. On rocks or logs in the lower intertidal to a depth of 5 m; Spring, Summer, Fall and Winter; 6th Spur to marker 37; >–25 ‰; 16–<10° C.
- Ulva fenestrata* Postels & Ruprecht. On rocks or logs in the lower intertidal to a depth of 4 m; Summer, Fall and Winter; 6th Spur to Port Docks; 33–25 ‰; 12–10° C.
- Ulva lobata* (Kützting) Setchell & Gardner. On rocks or epiphytic in the lower intertidal; Spring, Summer, and Fall; 6th Spur to Newport Bridge; 33–25 ‰; 12–<10° C.
- Ulva rigida* C. Agardh. On rocks and wood or epiphytic in the intertidal and subtidal; Summer, Fall and Winter; 6th Spur to Port Docks; >33–25 ‰; 12–<10° C.
- Ulva taeniata* (Setchell) Setchell & Gardner. On rocks in the lower intertidal to a depth of 2 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; >33–25 ‰; 16–>10° C.
- Ulvaria fuscum* (Postels & Ruprecht) Bliding. On rocks in the mid-intertidal; Fall; 1st Spur to Newport Bridge; 33–30 ‰; 12–10° C.
- Ulvaria oxyspermum* (Kützting) Bliding. On rocks, logs, sticks, or entangled with other algae or salt grass in the upper and mid-intertidal; Spring, Summer, Fall and Winter; 1st Spur to Toledo Bridge; >33–<5 ‰; >20–<10° C.
- Urospora penicilliformis* (Roth) Areschoug. On rocks in the upper intertidal; Summer; 6th Spur only; 33–30 ‰; 16–10° C.

Phaeophyta

- Alaria marginata* Postels & Ruprecht. On rocks, or logs lower intertidal to a depth of 3 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to Port Docks; >33–25 ‰; 16–<10° C.
- Desmarestia munda* Setchell & Gardner. On rocks and logs in the lower intertidal to a depth of 4 m; Spring, Summer, and Fall; 6th Spur to marker 21; 33–25 ‰; 20–<10° C.
- Ectocarpus acutus* Setchell & Gardner var. *acutus*. Epiphytic on *Desmarestia* and *Alaria* in the lower intertidal; Spring; 6th Spur to Coast Guard Dock; 33–30 ‰; 12–<10° C.

- Ectocarpus confervoides* (Roth) LeJolis f. *confervoides*. Epiphytic on larger brown algae in the lower intertidal; Spring; 3rd Spur to Coast Guard Dock; 33–30 ‰; 12–<10° C.
- Ectocarpus parvus* (Saunders) Hollenberg. Epiphytic on *Desmarestia* or *Laminaria saccharina* in the lower intertidal to subtidal; Fall and Winter; 1st Spur to Port Docks; 33–25 ‰; 12–<10° C.
- Egregia menziesii* (Turner) Areschoug subsp. *menziesii*. On rocks in the lower intertidal to a depth of 3 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to Coast Guard Dock; 33–25 ‰; 16–<10° C.
- Elachistea fucicola* (Velley) Areschoug. Epiphytic on *Fucus* in the upper intertidal; Spring, Summer, Fall, and Winter; 6th Spur to marker 37; >33–5 ‰; >20–<10° C.
- Fucus evanescens* Gardner f. *oregonensis*. On rocks or mud flats in the middle intertidal. On the mud flats in some locations this species exists as sterile mats; Spring, Summer, Fall and Winter; markers 27 to 47; >35–<5 ‰; >20–<10° C.
- Fucus distichus* L. subsp. *edentatus* (De la Pylaie) Powell. On rocks or logs in the upper intertidal; Spring, Summer, Fall and Winter; 6th Spur to marker 27; 33–25 ‰; 16–<10° C.
- Giffordia granulosa* (J. E. Smith) Hamel. On rocks in the lower intertidal; Spring and Winter; 1st Spur to Newport Bridge; 33–25 ‰; 14–<10° C.
- Giffordia granulosa* (Setchell & Gardner) Hollenberg & Abbott. On log floats; Winter; Coast Guard Dock to marker 21; 29–25 ‰; 11–<10° C.
- Giffordia mucronata* (Saunders) Kjeldsen & Phinney, comb. nov. (*Ectocarpus mucronatus* Saunders). On logs and epiphytic on *L. sinclairii* in the lower intertidal and subtidal; Spring; 6th Spur to Coast Guard Dock; 33–29 ‰; 16–<10° C.
- Giffordia oviger* (Harvey) Hollenberg & Abbott. On rocks in the upper intertidal; Winter; 1st Spur to Newport Bridge; 32–25 ‰; 12–<10° C.
- Haplospogonidion gelatinosum* Saunders. On rocks in the upper intertidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–25 ‰; 17–<10° C.
- Haplogloia andersonii* (Farlow) Levring. On rocks in the middle intertidal; Spring; 1st Spur to Newport Bridge; 33–25 ‰; 20–<10° C.
- Hecatonema variable* Setchell & Gardner. On pneumatocysts and stipes of *Nereocystis*, and lamina of *Hedophyllum*, and *Laminaria*; Winter; 1st Spur to Newport Bridge; 30–25 ‰; 12–<10° C.
- Hedophyllum sessile* (C. Agardh) Setchell, in Collins, Helden, & Setchell. On rocks in the middle intertidal; Spring, Summer, Fall and Winter; 6th Spur to marker 12; 35–27 ‰; 16–>10° C.
- Heterochordaria abietina* (Ruprecht) Setchell & Gardner. On rocks in the upper intertidal; Spring, Summer, Fall and Winter; 6th Spur to North Jetty flat; 32–25 ‰; 12–<10° C.
- Laminaria saccharina* Lamouroux f. *saccharina*. On rocks or log floats in the lower intertidal to a depth of 3 m in the subtidal; Spring, Summer, Fall and Winter; 3rd Spur to marker 21; 33–25 ‰; 16–<10° C.
- Laminaria setchellii* Silva. On rocks in the lower intertidal or subtidal to a depth of 1 m; Spring, Summer, Fall and Winter; 6th Spur to North Jetty flat; 33–30 ‰; 14–<10° C.
- Laminaria sinclairii* (Harvey ex Hooker f. & Harvey) Farlow, Anderson, & Eaton. On rocks in the lower intertidal to a depth of 1 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to North Jetty flat: 33–28 ‰; 15–<10° C.
- Leathesia difformis* (L.) Areschoug. On rocks or epiphytic in the upper intertidal; Spring and Summer; 3rd Spur to North Jetty flat; 33–30 ‰; 16–<10° C.
- Nereocystis luetkeana* (Mertens) Postels & Ruprecht. On rocks in the subtidal to a depth of 5 m. Dense stands develop each spring and persist until November on the spurs of the south jetty; Spring, Summer, Fall and Winter; 6th Spur to marker 12; 33–30 ‰; 16–<10° C.

- Pelvetiopsis limitata* Scagel f. *limitata*. On rocks high in the upper intertidal; Summer and Fall; 3rd Spur to Newport Bridge; 33–29‰; 13–<10° C.
- Petalonia debilis* (C. Agardh) Derbes & Solier f. *debilis*. On rocks, logs or *Zostera* in the upper to the lower intertidal; Spring, Summer, Fall and Winter; 6th Spur to marker 12; 33–25‰; 16–<10° C.
- Phaeostrophion irregulare* Setchell & Gardner. On rocks or logs in the middle intertidal; Spring, Summer, Fall and Winter; 3rd Spur to Newport Bridge; 33–25‰; 16–<10° C.
- Pilayella littoralis* (Lyngbye) Kjellman. On log floats; Spring; Coast Guard Dock to Port Docks; 32–30‰; 11–<10° C.
- Sargassum muticum* (Yendo) Fensholt. On rocks subtidal to a depth of 4 m. The most luxuriant growth occurs on the leeward side of the spurs on the south jetty; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–30‰; 16–<10° C.
- Scytosiphon lomentaria* (Lyngbye) J. Agardh f. *lomentaria*. On rocks or logs in the lower intertidal; Summer and Fall; 3rd Spur to marker 21; 33–29‰; 16–<10° C.
- Soranthera ulvoidea* Postels & Ruprecht. Epiphytic on *Rhodomela* in the upper intertidal; Summer; 6th Spur to North Jetty flat; 33–30‰; 12–<10° C.
- Streblonema acidioides* Setchell & Gardner var. *pacificum* Setchell & Gardner. Epiphytic on *Hedophyllum*, *Laminaria* and *Alaria*; Fall and Winter; 6th Spur to Newport Bridge; 33–25‰; 12–<10° C.

Rhodophyta

- Ahnfeltia gigartinoides* J. Agardh. On rocks in the lower intertidal; Spring; 6th Spur to 3rd Spur; 33–30‰; 12–10° C.
- Antithamnion kylinii* Gardner. On log floats; Summer; Coast Guard Dock to Port Docks; 33–30‰; 12–10° C.
- Antithamnion pacificum* (Harvey) Kylin. On log floats; Spring and Summer; 1st Spur to Port Docks; 33–29‰; 12–10° C.
- Bangia fuscopurpurea* Harvey. On piling or rocks in the upper intertidal; Spring, Summer, Fall and Winter; 1st Spur to Port Docks; 33–27‰; 16–<10° C.
- Bossiella dichotoma* (Manza) Silva. On rocks in the lower intertidal to a depth of 2 m; Spring, Summer, Fall and Winter; 6th Spur to 1st Spur; 33–26‰; 12–10° C.
- Botryoglossum ruprechtiana* (J. Agardh) De Toni. On rocks; subtidal; Summer; 6th Spur only; 33–29‰; 12–10° C.
- Callithamnion pikeanum* Harvey. On rocks or epiphytic in the lower intertidal; Spring, Summer, Fall and Winter; 6th Spur to 1st Spur; 33–30‰; 12–10° C.
- Callophyllis violacea* J. Agardh. Subtidal on rocks to a depth of 5 m; Spring, Summer, Fall and Winter. 6th Spur to 1st Spur; 33–28‰; 16–<10° C.
- Ceramium californicum* J. Agardh. Found only on *Gracilariopsis* as an epiphyte in the lower intertidal to a depth of 3 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–30‰; 16–<10° C.
- Ceramium gardneri* Kylin. On rocks in the lower intertidal; Spring; 6th Spur to 3rd Spur; 32–28‰; 12–<10° C.
- Ceramium eatonianum* (Farlow) De Toni. On rocks in the lower intertidal to a depth of 2 m in the subtidal; Winter; 6th Spur to North Jetty flat; 33–25‰; 16–10° C.
- Ceramium pacificum* (Collins) Kylin. On rocks in the lower intertidal; Summer, 6th Spur to North Jetty flat; 32–30‰; 12–<10° C.
- Constaninea simplex* Setchell. Collected on several occasions only during the spring of 1964. On rocks in the lower intertidal; Spring, Summer, Fall and Winter; 3rd Spur to 1st Spur; 33–30‰; 12–10° C.
- Corallina officinalis* L. var. *chilensis* (Harvey) Kützinger. On rocks in the middle intertidal to a depth of 3 m; Summer; 6th Spur to 1st Spur; 33–30‰; 12–10° C.

- Corallina vancouveriensis* Yendo. On rocks, the encrusting basal portion present all year in the upper intertidal to a depth of 3 m in the subtidal; Summer, Fall and Winter; 6th Spur to 1st Spur; 33–30 ‰; 12–<10° C.
- Cryptopleura violacea* (J. Agardh) Kylin. Epiphytic on red algae in the lower intertidal to a depth of 2 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–30 ‰; 12–10° C.
- Cryptosiphonia woodii* J. Agardh. On rocks in the upper to lower intertidal; Spring, Summer, Fall and Winter; 6th Spur to Coast Guard Dock; 33–27 ‰; 16–<10° C.
- Cumagloia andersonii* (Farlow) Setchell & Gardner in Gardner. On rocks in the upper intertidal; Spring and Summer; 6th Spur to 1st Spur; 33–30 ‰ 15–10° C.
- Delesseria decipiens* J. Agardh. On rocks in the lower intertidal to a depth of 2 m in the subtidal; Spring; 6th Spur to Newport Bridge; 33–30 ‰; 16–10° C.
- Endocladia muricata* (Postels & Ruprecht) J. Agardh. On rocks in the upper intertidal; Spring, Summer, Fall and Winter; 6th Spur to 1st Spur; 33–28 ‰; 16–<10° C.
- Erythrophyllum delesserioides* J. Agardh. On rocks in the subtidal to a depth of 3 m; Summer; 6th Spur only; 33–29 ‰; 15–<10° C.
- Gelidium coulteri* Harvey. On rocks in the middle intertidal; Fall and Winter; 6th Spur to 3rd Spur; 33–28 ‰; 16–<10° C.
- Gigartina agardhii* Setchell & Gardner. On rocks in the upper intertidal; Spring, Fall and Winter; 6th Spur to Newport Bridge; 33–29 ‰; 16–<10° C.
- Gigartina californica* J. Agardh. On rocks in the lower intertidal to a depth of 3 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–25 ‰; 16–10° C.
- Gigartina cristata* (Setchell) Setchell & Gardner. On rocks in the upper intertidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–25 ‰; 16–<10° C.
- Gigartina harveyana* (Kützinger) Setchell & Gardner. On rocks in the lower intertidal and subtidal; Fall and Winter; 6th Spur to Newport Bridge; 32–26 ‰; 12–10° C.
- Gigartina papillata* (C. Agardh) J. Agardh. On rocks in the upper intertidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–25 ‰; 15–<10° C.
- Gigartina spinosa* (Kützinger) Harvey. On rocks in the lower intertidal to a depth of 1 m in the subtidal; Summer, Fall and Winter; 6th Spur to 1st Spur; 33–26 ‰; 14–<10° C.
- Gigartina volans* (C. Agardh) J. Agardh. On rocks in the lower intertidal to a depth of 2 m in the subtidal; Spring, Summer and Fall; 6th Spur to 1st Spur; 33–30 ‰; 15–10° C.
- Gracilaria sjoestedtii* (Kylin) Papenfuss. On rocks and shells in the lower intertidal to a depth of 4 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–26 ‰; 16–<10° C.
- Gracilaria verrucosa* (Hudson) Papenfuss. Massive patches in protected mud flats in the mid-intertidal; Spring and Winter; markers 27 to 37; 33–20 ‰; 20–<10° C.
- Grateloupia doryphora* (Montagne) Howe. On rocks in the lower intertidal; Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–30 ‰; 12–10° C.
- Gymnogongrus leptophyllus* J. Agardh. On rocks in the lower intertidal to a depth of 2 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–25 ‰; 16–<10° C.
- Gymnogongrus linearis* (Turner) J. Agardh. On rocks in the lower intertidal; Spring, Summer, Fall and Winter; 6th Spur to North Jetty flat; 33–25 ‰; 16–<10° C.

- Halymenia californica* Smith & Hollenberg. On rocks in the lower intertidal; Spring, Summer and Fall; 6th Spur to Newport Bridge; 33–30‰; 15–<10° C.
- Hymeneia flabelligera* (J. Agardh) Kylin. On rocks in the lower intertidal to a depth of 2 m in the subtidal; Winter; 6th Spur only; 32–28‰; 12–11° C.
- Hymeneia multiloba* (J. Agardh) Kylin. On rocks in the lower intertidal to a depth of 2 m in the subtidal; Fall and Winter; 6th Spur only; 33–28‰; 12–10° C.
- Iridaea cordata* (Turner) Abbott var. *cordata*. On rocks lower intertidal to a depth of 2 m in the subtidal; Summer, Fall and Winter; from 6th Spur to Newport Bridge; 33–28‰; 15–<10° C.
- Iridaea flaccida* (Setchell & Gardner) Hollenberg & Abbott. On rocks lower intertidal to a depth of 2 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–30‰; 15–<10° C.
- Iridaea heterocarpa* Postels & Ruprecht. On rocks upper to middle intertidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–25‰; 16–<10° C.
- Laurencia spectabilis* Postels & Ruprecht. On rocks in the lower intertidal to a depth of 2 m; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–28‰; 16–<10° C.
- Membranoptera multiramosa* Gardner. On rocks in the lower intertidal or subtidal; Spring and Summer; 6th Spur to Port Docks; 33–28‰; 16–10° C.
- Microcladia borealis* Ruprecht. On rocks and epiphytic in the lower intertidal; Spring, Summer, Fall and Winter; 6th Spur to 1st Spur; 32–26‰; 16–<10° C.
- Neodilsea americana* Abbott. On rocks in the lower intertidal and subtidal; Summer; 6th Spur to 1st Spur; 33–29‰; 14–<10° C.
- Odonthalia floccosa* (Esper) Falkenberg. On rocks in the lower intertidal to a depth of 3 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to Coast Guard Dock; 33–26‰; 16–<10° C.
- Odonthalia washingtoniensis* Kylin. On rocks in the lower intertidal to a depth of 2 m in the subtidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–27‰; 16–<10° C.
- Opuntia californica* (Farlow) Kylin. On rocks in the lower intertidal; Spring; 6th Spur to 3rd Spur; 33–30‰; 12–10° C.
- Pikea pinnata* Setchell. On rocks in the lower intertidal; Spring and Summer; 6th Spur to 1st Spur; 33–30‰; 16–<10° C.
- Platythamnion pectinatum* Kylin. On rocks or logs in the lower intertidal to a depth of 5 m in the subtidal. In the early spring, it is in the intertidal but is found only subtidally during the summer and fall; Spring, Summer, Fall and Winter; 6th Spur to marker 21; 33–30‰; 12–10° C.
- Platythamnion villosum* Kylin. On rocks in the lower intertidal and subtidally; Spring; 6th Spur to 3rd Spur; 33–29‰; 12–<10° C.
- Plocamium pacificum* Kylin. On rocks in the lower intertidal to a depth of 2 m in the subtidal; Fall and Winter; 6th Spur to 3rd Spur; 32–27‰; 11–<10° C.
- Polyneura latissima* (Harvey) Kylin. On rocks, logs or epiphytic in the lower intertidal to a depth of 3 m. Common in the spring and summer of 1964, rare in spring and summer of 1965, but common in the spring of 1966; Spring, Summer and Fall; 6th Spur to Port Docks; 33–29‰; 14–<10° C.
- Porphyra lanceolata* (Setchell & Hudson) Smith & Hollenberg. On rocks in the upper intertidal; Fall, Winter and Spring; 3rd Spur to Newport Bridge; 33–25‰; 13–<10° C.
- Porphyra nereocystis* Anderson, in Blankinship & Keeler. Rare, found only on *Nereocystis* in wash; Spring; North of Jetty flat to Newport Bridge; 33–28‰; 16–10° C.
- Porphyra perforata* J. Agardh f. *perforata*. On rocks in the upper intertidal; Spring, Summer, Fall and Winter; 3rd Spur to marker 12; 33–25‰; 16–<10° C.
- Porphyra smithii* Hollenberg & Abbott. Epiphytic in middle intertidal; Spring, Summer and Fall; 6th Spur to North Jetty flat; 33–28‰; 12–<10° C.

- Porphyra thruetii* (Setchell & Hudson) Smith & Hollenberg. On rocks in the upper intertidal; Summer; 3rd Spur to North Jetty flat; 33–30‰; 12–10° C.
- Porphyrella gardneri* Smith & Hollenberg. On *Phyllospadix* or *Laminaria sinclairii* in the lower intertidal to subtidal; Summer and Fall; 6th Spur to 1st Spur; 33–30‰; 15–10° C.
- Polysiphonia collinsii* Hollenberg. On rocks in the lower intertidal; Spring; 6th Spur to North Jetty flat; 33–28‰; 11–10° C.
- Polysiphonia decussata* Hollenberg. Epiphytic on *Enteromorpha* in the middle intertidal; Summer; markers 37 to 47; 15–10‰; 20–17° C.
- Polysiphonia pacifica* Hollenberg. On rocks or logs in the lower intertidal to the subtidal; Spring, Summer, Fall and Winter; 3rd Spur to marker 37; 33–10‰; >20–<10° C.
- Polysiphonia paniculata* Montagne. On rocks or logs in the lower intertidal to a depth of 3 m; Spring, Summer, Fall and Winter; 6th Spur to marker 47; >33–<5‰; >20–<10° C.
- Prionitis andersonii* Eaton. On rocks in the lower intertidal; Spring, Summer, Fall and Winter; 3rd Spur to Newport Bridge; 33–28‰; 16–<10° C.
- Prionitis lanceolata* Harvey. On rocks in the upper intertidal; Spring and Winter; 6th Spur to North Jetty flat; 33–26‰; 11–<10° C.
- Prionitis lyallii* Harvey. On rocks in the middle intertidal; Spring and Winter; 6th Spur to North Jetty flat; 33–30‰; 11–<10° C.
- Pterosiphonia bipinnata* (Postels & Ruprecht) Falkenberg. On rocks in the lower intertidal to subtidal; Spring and Summer; 6th Spur to Newport Bridge; 33–28‰; 14–<10° C.
- Pterosiphonia dendroidea* (Montagne) Falkenberg. Epiphytic and on rocks in the lower intertidal to subtidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–28‰; 16–<10° C.
- Ptilota filicina* (Farlow) J. Agardh. On rocks in the lower intertidal; Spring, Summer, Fall and Winter; 6th Spur to 1st Spur; 32–26‰; 14–10° C.
- Rhodomela larix* (Turner) C. Agardh. On rocks in the upper intertidal; Spring, Summer, Fall and Winter; 6th Spur to Newport Bridge; 33–26‰; 16–<10° C.
- Rhodymenia pacifica* Kylin. On rocks in the subtidal to a depth of 3 m; Summer and Fall; 6th Spur to 1st Spur; 33–25‰; 15–<10° C.
- Schizymenia pacifica* Kylin. On rocks in the lower intertidal; Summer, Fall and Winter; 6th Spur to 3rd Spur; 33–26‰; 15–<10° C.
- Smithora naiadum* (Anderson) Hollenberg. Epiphytic on *Zostera* and *Phyllospadix* in the lower intertidal; Summer and Fall; 6th Spur to 1st Spur; 33–28‰; 16–10° C.

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CHROMOSOME COUNTS IN ERIOPHYLLUM AND OTHER HELENIEAE (COMPOSITAE)

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This paper presents chromosome counts obtained during long term investigations of species complexes in *Eriophyllum* and *Chaenactis*. Methods and the disposition of voucher specimens have been described previously (Mooring, 1966). I appreciate support afforded by the National Science Foundation and the comments of John Strother. Counts for *Eriophyllum lanatum* var. *obovatum*, *Chaenactis alpigena* and *Orochaenactis thysanocarpa* are first reports, and those for all taxa but *E. lanatum* var. *integrifolium* ($2n = 16$ II), *E. confertiflorum* var. *tanacetiflorum*, *E. latilobum*, *Chaenactis suffrutescens* and *Pseudobahia heermannii* are new chromosome numbers for these taxa (Table 1). The counts for the latter 5 taxa are second or third reports.

My data for *Eriophyllum lanatum*, *E. confertiflorum*, and *E. latilobum* agree with and supplement those of Carlquist (1956) and Mooring (1966), but those for two other species of *Eriophyllum* differ. Carlquist reported $n = 16$ for *E. jepsonii*, whereas I found that $n =$ ca 32 to 42. My 11 counts come from 4 of the 5 known stations of this comparatively rare species, including a transect through the Arroyo del Puerto locality in which Carlquist obtained his material. Some individuals had the equivalent of 32 to 34 II, others probably had additional chromosomes. Meiotic irregularities and the absence of anaphase and telophase stages prevented more exact determination. Constance (1937) and Munz (1959) observed that *E. jepsonii* is in many ways intermediate between *E. lanatum* and *E. confertiflorum*, and Munz suggested a possible origin by interspecific hybridization. The meiotic irregularities may therefore reflect a hybrid derivation, the effects of polyploidy, or both. The biology of this species and its relationship to other species continue to be studied. In contrast to *E. jepsonii*, the 13 samples of *E. staechadifolium* furnished excellent meiotic cells, all of which showed 15 II, whereas Carlquist (1956) reported 16 II. John Strother also determined $n = 15$ for this species (Red Rock Island, Contra Costa Co., *Ferlatte and Moe 1251*, UC). This study continues, as the populations sampled did not include any visited by Carlquist.

The counts of 6 II for the relatively infrequently encountered *Chaenactis alpigena* and *C. suffrutescens* conform to the pattern of $n = 6$ in strongly perennial species of this genus (Raven and Kyhos, 1961; Mooring, 1965). Curiously, many of the *C. suffrutescens* fruits were empty, and germination of apparently viable ones, when tested in the garden, was a fraction of one per cent. The count of 9 II for the monotypic *Orochaenactis* was no surprise. Despite its generic name and

TABLE 1. CHROMOSOME COUNTS

Collection numbers are my own. Numbers in parentheses indicate number of individuals counted, if more than one. Locations are approximate.

- Eriophyllum lanatum* (Pursh) Forbes
 var. *arachnoideum* (Fisch. & Avé-Lall.) Jepson. $2n = 16$ II. California Sonoma Co., Jenner, 2223. $2n = 24$ II. California. Sonoma Co., Santa Rosa, 1907.
 var. *croceum* (Greene) Jepson. $2n = 8$ II (3). California. Tulare Co., Mineral King, 2237.
 var. *cuneatum* (Kell.) Jepson. $2n = 8$ II (3). California. Plumas Co., Quincy, 2027.
 var. *grandiflorum* (Gray) Jepson. $2n = 32$ II. California. Tehama Co., Paskenta, 2054.
 var. *integrifolium* (Hook.) Smiley. $2n = 16$ II (2). Idaho. Gem Co., Emmett, 2129. $2n = 24$ II (2). Washington. Yakima Co., Satus Pass, 1612. $2n = 32$ II or ca. 32 II (3). Oregon. Wasco Co., The Dalles, 1620.
 var. *lanceolatum* (Howell) Jepson. $2n = 16$ II. California. Siskiyou Co., Somesbar, 2947.
 var. *leucophyllum* (DC.) W. R. Carter. $2n = 8$ II. Washington. Kittitas Co., Cle Elum, 1597.
 var. *obovatum* (Greene) Hall. $2n = 8$ II (4). California. Kern Co., Alta Sierra, 2236, and San Bernardino Co., Running Springs, 2524.
Eriophyllum confertiflorum (DC.) Gray. $2n = 24$ II. California. Mariposa Co., Bagby, 2346.
 var. *tanacetiflorum* (Greene) Jepson. $2n = 32-34$ II (3). California. Mariposa Co., Bagby-Coulterville, 2013, 2016.
Eriophyllum jepsonii Greene. $2n = 32-42$ II (11). California. Alameda Co., Arroyo Mocho, 2436. Contra Costa Co., Mitchell Creek Canyon, 2331. San Benito Co., Antelope Fire Station, 2229, and Emmett, 2371. Stanislaus Co., Arroyo del Puerto, 2000, 2176, 2193, 2194, 2402.
Eriophyllum latilobum Rydberg. $2n = 16$ II (5). California. San Mateo Co., Hillsborough, 1961.
Eriophyllum staechadifolium Lagasca. $2n = 15$ II (13). California. Humboldt Co., Rockport, 2501. Marin Co., Marshall, 2221. Mendocino Co., Elk, 2503. Monterey Co., Carmel Highlands, 2881, and Point Sur, 2883. San Mateo Co., Half Moon Bay. Santa Cruz Co., Davenport, 2884.
Chaenactis alpigena C. W. Sharsmith. $2n = 6$ II (3). California. Alpine Co., Round Top Lake, 3008.
Chaenactis suffrutescens Gray. $2n = 6$ II. California. Trinity Co., Coffee Creek Ranger Station, 1721.
Orochaenactis thysanocarpa (Gray) Cov. $2n = 9$ II. California. Tulare Co., Quaking Aspen, 2530.
Pseudobahia heermannii (Dur.) Rydberg. $2n = 3$ II. California. Mariposa Co., Bootjack, 2010.

placement in the Helenieae the species does not resemble any *Chaenactis* in external morphology, pollen character, or chromosome number. The count of 3 II for *Pseudobahia heermannii* agrees with previous ones from the same geographic area by Carlquist (1956), whereas Strother (1972) reported 4 II from a Tulare Co. population. Carlquist (1956) reported counts of $n = 4$ from *P. bahiaefolia* however, and Munz (1959) observed that these species are "possibly insufficiently distinct". Further study of both might prove interesting.

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NEW RECORDS OF MYXOMYCETES FROM CALIFORNIA V.

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To date, 222 species of slime molds have been reported from California (Kowalski, 1970a; 1970b; 1972; Kowalski and Curtis, 1970). In this paper nine new records are discussed, bringing the total to 231. Thus, over 50% of the known species of slime molds (Martin and Alexopoulos, 1969) have been found in California. This seemingly high percentage is due to two factors: 1) California contains many varied habitats and thus species from different ecological niches and 2) Myxomycetes are generally cosmopolitan in distribution.

All collections listed have been deposited in the Herbarium of the University of California (UC). Nomenclature follows Martin and Alexopoulos (1969). Collection numbers are my own. This investigation was supported by the National Science Foundation grant GB-28653.

LICEACEAE

Licea castanea G. Lister. Inner surface of decaying bark, Pine Creek Ranch, 24 miles north of Chico, Butte Co., 10963, Dec. 12, 1969, 10981 and 10984, Jan. 9, 1970; dead wood, Lower Bidwell Park, Chico, Butte Co., 3872, March 27, 1965; decayed bark, Woodson Bridge State Park, Tehama Co., 9656, April 29, 1967. In each of the above collections the substrate upon which *L. castanea* was growing was originally collected because it had another, larger myxomycetous species upon it. The minute sporangia of *L. castanea* were discovered later in the laboratory while the substrate was being scanned with a stereoscopic microscope. There

are numerous sessile species of *Licea* that have the peridium divided into distinct lobes. *Licea castanea* can be distinguished from these by the chestnut to light brown color of the peridium and the nearly smooth spores. In the United States *L. castanea* has been reported as far west as Kansas and is considered rare. Because of its small size, the sporangia being about 0.25 mm in diameter, it is easily overlooked.

Licea pedicellata (H. C. Gilbert) H. C. Gilbert. Bark of living *Quercus lobata* Neé in Lower Bidwell Park, Chico, Butte Co., 9887, 9890, 9892, 9894, Feb. 21, 1969; 11013, Jan. 28, 1970; 10266 and 10275, Jan. 30, 1970. All of these collections represent naturally developed fructifications. This is unusual for this species as it is mainly known from damp chambers. *Licea pedicellata*, *L. operculata* (Wingate) Martin, and *L. erecta* Thind and Dhillon are the only species of the genus that have stalked sporangia. *Licea pedicellata* can be distinguished from *L. operculata* by the absence of a distinct sporangial lid. It differs from *L. erecta* by the presence of platelets in the peridium, sporangia 0.1–0.3 mm in diameter and spores 11–13 μ in diameter, while *L. erecta* lacks peridial platelets, has sporangia 0.3–0.4 mm in diameter and spores 14–15 μ in diameter. With the exception of spores 9–10 μ in diameter instead of the reported 12–13 μ , the description listed above fits the published descriptions perfectly. Since Martin and Alexopoulos (1969) state that on rare occasions the spores can be as small as 10 μ , I do not believe that this difference is of taxonomic significance. Prior to this report, *L. pedicellata* was collected only as far west as Texas. However, with diligent damp chamber work, this minute species should be found throughout the United States.

CRIBRARIACEAE

Cribraria dictyospora Martin and Lovejoy. Decayed wood, 6718, Mt. Shasta, Siskiyou Co., 7,200 ft. elev., July 5, 1967, and 7538, King's Creek, Lassen Volcanic National Park, 7,200 ft. elev., July 27, 1968. This taxon can be distinguished from other members of the genus by the relatively large, hazel sporangia that are up to 0.8 mm in diameter, with distinct basal cups containing dark radiating lines, as well as the large reticulate spores that are 8–9 μ in diameter. The spore reticulations in these two specimens are very distinct and most of the spores are 9 μ in diameter. Most species of *Cribraria* have spores about 6 μ in diameter. *Cribraria dictyospora* is an extremely rare species, previously reported only from Oregon.

TRICHIACEAE

Trichia verrucosa Berk. Decaying log, Big Lagoon School, Humboldt Co., 12111, Jan. 30, 1972. This species is easy to identify, being the only member of the genus with distinctly stalked sporangia and coarsely reticulate spores. Additional characteristics helpful in recognizing it are the presence of capillitial threads with short tapering apices and the tendency for fusion of the stalks so that the sporangia form in small

clusters. This species has been reported from many areas of the world, but nowhere does it appear to be common. In the United States it has been reported only from Washington and Oregon.

STEMONITACEAE

Barbeyella minutissima Meylan. On a leafy liverwort, 10427, MacKerricher Beach State Park, Mendocino Co., March 23, 1970: decayed wood, 11884, Serene Lake, Placer Co., 6,700 ft. elev., June 28, 1971, 11885, Luther Pass, El Dorado Co., 7,700 ft. elev., June 19, 1971; bryophytes on dead wood, 12120 and 12121, Big Lagoon School, Humboldt Co., Jan. 30, 1972. *Barbeyella* is monotypic and is easily identified by its minutely stalked sporangia less than 0.2 mm in diameter. The few capillitial threads are attached at their apices to the large petaloid lobes of the peridium. Because of the small sporangia, these collections were discovered accidentally in the laboratory by scanning the substrate with a stereoscopic microscope. This species is known only from a few locations in the world. I have, however, found it many times in Washington and predict that it can be found with regularity if lignicolous bryophytes are scanned carefully in the laboratory.

Macbrideola decapillata H. C. Gilbert. Bark of living *Quercus lobata* Neé, Lower Bidwell Park, Chico, Butte Co., 9665, Feb. 5, 1967, 9724, Nov. 23, 1966, 9873, Dec. 22, 1966, 9875, Feb. 3, 1967, 10274, Jan. 30, 1970. Because of the small sporangia that are less than 100 μ in diameter, it is difficult to observe *M. decapillata* in the field. My collections were obtained by collecting bark that had *Physarum crateriforme* Petch growing on it and searching for *M. decapillata* in the laboratory with a stereoscopic microscope. I have made many collections of this species, but list five here for the sake of brevity. This species differs from other members of the genus by its fugacious peridium, tapering capillitial threads and uniformly warted spores that exceed 8.0 μ in diameter. *M. decapillata* is known only from scattered localities in the United States, but it is probably often overlooked because of its small size.

Lamproderma arcyryonema Rost. On fallen conifer twigs, Panther Meadows Campground, Siskiyou Co., 7,600 ft. elev., 3682, June 25, 1966. There are several characteristics that distinguish this species from the closely related *L. biasperosporum* Kowalski. In *L. arcyryonema* the capillitium forms a rigid intricate net with many circinate-flexuous threads and is dark brown throughout. Thus, it appears reddish brown when the peridium is removed and the spores have been blown out. In *L. biasperosporum* the capillitium forms a very weak, lax net with little branching and anastomosing. The threads are straight, not circinate-flexuous, and the extremities are colorless. Thus, it appears whitish when the peridium is removed and the spores have been blown out. The sporangia of *L. arcyryonema* are 0.5 mm or more in diameter and clustered while those of *L. biasperosporum* are 0.5 mm or less in diameter and widely scattered. *L. arcyryonema* is probably the most common species in the genus, but it appears to be rare in California.

PHYSARACEAE

Badhamia obovata (Peck) S. J. Smith. Pygmy Forest near Van Damme State Park, Mendocino Co., March 22, 1970, 10285 on a decaying leaf and 10286 on decaying bark. *Badhamia obovata* is readily separated from the other species in the genus by its stipitate habit, distinctive cylindrical columella, and spores that are often strikingly reticulate. Although it is the most common member of the genus, it appears to be rare in California.

DIDYMIACEAE

Mucilago crustacea Wiggers. On the stem of living *Rhus diversiloba* T. & G., 11886, Lower Bidwell Park, Chico, Butte Co., Dec. 12, 1970. This taxon is extremely easy to identify as it is the only known slime mold that is aethaloid and has crystalline lime in the peridium. Although *M. crustacea* appears to be rare in California, it is cosmopolitan and in most regions of its range it seems to be very common.

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A DISTINCTIVE NEW CALOCHORTUS (LILIACEAE) FROM
MARIN COUNTY, CALIFORNIA

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While it is not unusual for a new species of plants to be described from a state as well collected as California, it is remarkable that a plant as distinctive as the species of *Calochortus* described herein has escaped discovery for so long, since it is from an area that has been given considerable attention (Howell 1970, Peñalosa 1963). In overall appearance it is easily recognized and in detail it shows a combination of characteristics unique in the genus. It is in fact so distinctive that its existence challenges the currently accepted infrageneric classification.

Calochortus tiburonensis A. J. Hill, sp. nov.

Bulbi tunica, saltem apud bulbos maiores, fibroso-reticulata; folium basale unicum, planum, usque ad post anthesin tempum viride; flores late campanulati, erecti; petala pallida flavo-viridia, fimbriata, maculis

guttisque badiis ornata, maxima parte centrali deltoideo-ovata, apice acuta vel acuminata, late unguiculata, glandula infra medium posita, superficie nuda, pilis gracilibus proxime supra atque utroque et lateraliter fere usque ad apicem barbata, profunde lunata, versus petali apicem arcuata, depressa, margine inferiori membrano lato, ea superiori seriebus duabus vel pluribus processibus applanatis instructa; ovarium lineare, non alatum; fructus fusiformi-prismaticus, in transectione triangularis, erectus; semina parum compressa, asymmetrica vel plus minusve rhomboideo-prismatica, atropurpurea, testa sexangulariter reticulata.

Bulb ovoid, with coat membranous or fibrous-reticulate in larger bulbs; stems slender, to 5 dm or more in height, usually branched, not bulbiferous; basal leaf single, linear-oblong, to 17 mm or more in width and to 6 dm or more in length, usually green at anthesis; cauline leaves linear, involute, reduced upward; inflorescences bracteate, the bracts similar to the cauline leaves, the flowers usually in pairs or less frequently three from the ultimate axils; flowers broadly campanulate in outline, erect, the petals light yellow-green, flecked to varying degrees with purplish-brown and with more or less conspicuous transverse arching bands of the same color, the most prominent of which is near the mid-point; sepals about equalling or slightly longer than the petals, lance-oblong, attenuate, glabrous, pale yellow green, flecked, streaked, and veined with purplish-brown; petal blade deltoid-ovate, rounded laterally, acute to acuminate above and very broadly clawed below, with a conspicuous complex glandular area below the middle; basal portion of petal, including the glandular region, extending outward more or less at a right angle from the vertical axis of the flower, the apical portion curving abruptly upward to an erect position; petals long-fimbriate from above the claw to near the tip with long, slender hairs similar to the lateral fimbriations; gland deeply crescent-shaped, about one-half the width of the petal, depressed, the surface naked, bordered below with a broad, erect, upward arching, erose and minutely papillose membrane, bordered above with two or more indistinct rows of transversely flattened processes, which are often engaged and sometimes divided apically, the processes similar in appearance to the lower membrane, but less broad with respect to the vertical dimension of the lower membrane; stamens about equal to or slightly shorter than the petals, the filaments parallel to the flower axis to near tip, then divergent; anthers slightly longer than the filaments prior to shedding of pollen, narrowly lanceolate, short acuminate, divergent from the flower axis; ovary linear, not winged, tapering to a persistent trifid stigma; stigma-branches linear, strongly divergent and curved; fruit fusiform-linear, acute, triangular in cross-section, several times the length of the pistil at anthesis, erect; seeds in two closely appressed rows in each locule, slightly compressed, irregular or roughly rhomboid-prismatic in shape, dark purplish, with a hexagonally reticulate coat. Figure 1.

TYPE. *A. J. Hill 51239.4A*, north slopes of Ring Mt., Tiburon Peninsula, Marin Co, California, elevation ca 110 m, June 19, 1972 (UC 1393720—holotype; isotypes to be distributed to US, UCLA, and RSA).

Known only from the vicinity of the type locality in an area about 0.8 kilometers across. It is found on rocky slopes of serpentine and serpentine derived soils. The area is open, with a variety of grasses and other annual and perennial herbs. There are limited areas of shrubs and wind-swept trees, but no plants of this *Calochortus* were seen growing in these areas. The site of the type locality is privately owned and there is considerable interest in including it in an adjacent open space area slated to be purchased by the city of Tiburon.

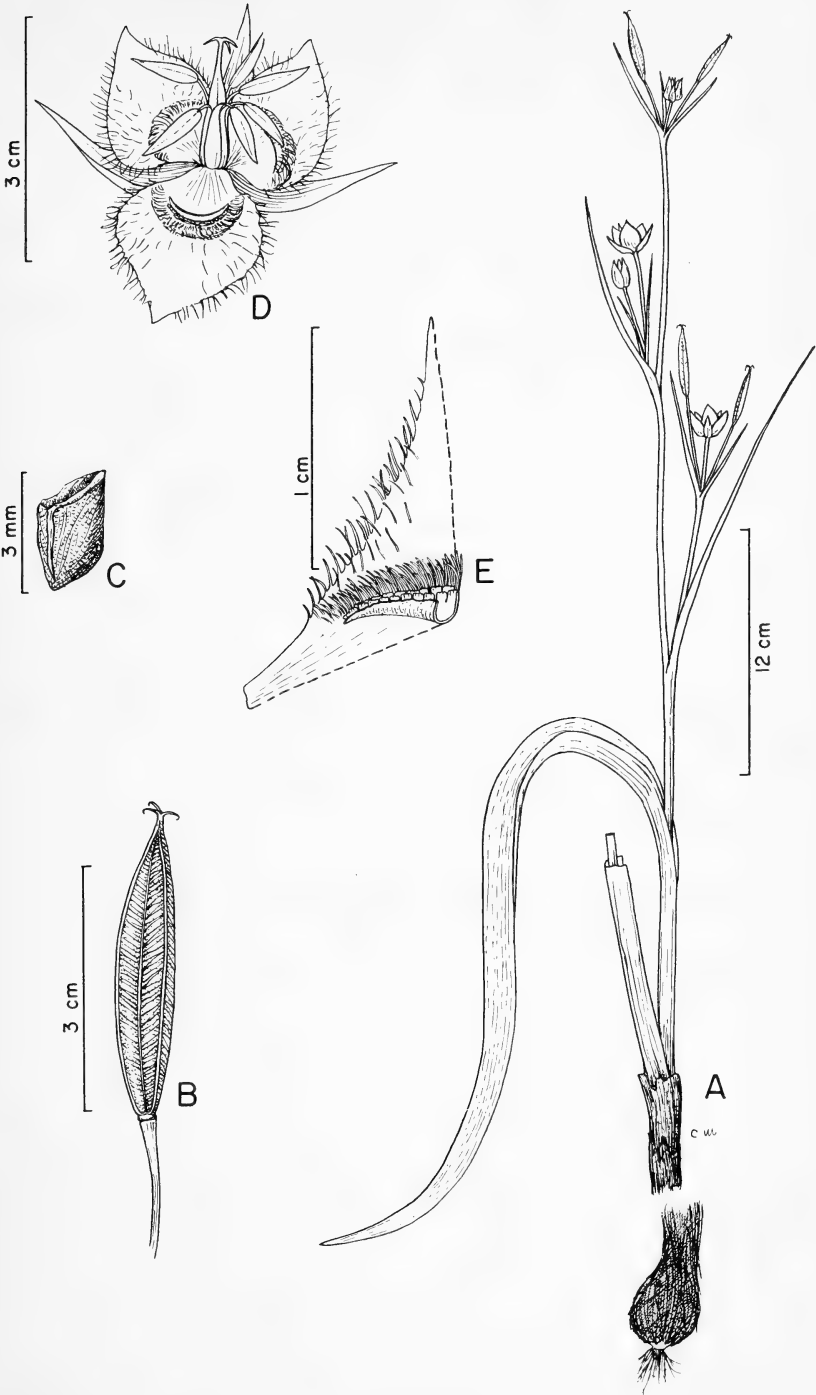
In its combination of morphological features *Calochortus tiburonensis* is unlike any other species of the genus. It does not fall within any of the three sections of the genus as delimited in the most recent monographic treatment (Ownbey 1940), but shows features that are normally found in two of these sections. The flat, usually single, rather persistent basal leaf would place it among the species of sections *Calochortus* (= *Eucalochortus*) or *Cyclobothra* and make it rather distinct from those of section *Mariposa*.

The fibrous-reticulate bulb coat, although not as reticulate as in many species of the section, and non-winged capsule could be considered sufficient evidence to place *Calochortus tiburonensis* in section *Cyclobothra*. The general coloration and shape of the flower, the petal margin and vestiture, and the habit of the plant also give the general appearance of some species of this section, such as *C. weedii*. However, the glandular area of the petal, which is prominently developed in the genus and appears to be of considerable diagnostic value, is definitely unlike that found in the species of section *Cyclobothra*. Moreover, it is quite similar to a type of gland found in species of section *Calochortus*, such as *C. tolmei*. The darkly pigmented, reticulate seed coat and only slightly compressed seeds are also typical of species of section *Calochortus*, although this type of seed may also be found among species of section *Cyclobothra*, the seeds of many of which have not yet been described.

Geographically, *Calochortus tiburonensis* also seems to occupy an intermediate position between the two sections. The nearest representative of section *Cyclobothra* is found 250 kilometers to the south of the Tiburon area, with the remaining species further to the south in California and in Mexico and Guatemala. The greatest species diversity in section *Calochortus* is in the Pacific Northwest with the number of species decreasing sharply south of the San Francisco Bay area. *Calochortus tiburonensis* occupies a position distinctly to the south of the center of diversity of section *Calochortus*.

The highly unusual combination of characteristics, geographic position, and localized occurrence of *C. tiburonensis* suggest the possibility, although remote, that it may be the result of hybridization. However,

FIG. 1. *Calochortus tiburonensis*: A, habit with portion of persistent previous year's stem and leaf shown on the left; B, mature fruit; C, seed; D, flower with forward petal bent down and forward for clarity; E, side view of one-half of petal in longitudinal section. (From collection A. J. Hill 51239.4)



aside from variations in the depth of the purplish pigmentation in the flowers and general size of the plants, the population appeared to be quite uniform on field examination and without any variations that would suggest hybridization. Examination of a scattered sample of immature capsules in the field did not reveal any with reduced seed set. Pollen fertility, as judged under the microscope when stained with cotton blue in lactophenol, was 96, 98, and 99 per cent in samples of 600 grains from a single flower each of three plants, which compares favorably with observations on other *Calochortus* species. In these preliminary studies, then, there is nothing to support the idea of hybridization, at least of recent occurrence.

The occurrence of this intermediate species does establish a closer relationship between the two sections than was previously recognized and challenges the concept of placing the two species groups in separate sections on a par with the third species group in the genus. It also challenges the idea of Hoover (1944) that they should possibly be placed in separate genera.

The existence of an unidentifiable *Calochortus* was apparently first noticed by Dr. Robert West and was subsequently seen by Mrs. J. C. Youngberg, Miss Annetta Carter, and Mrs. George Ellman. Miss Carter reported the occurrence of the *Calochortus* to the author. The credit for the actual discovery belongs to these persons whose interest in protecting the open space of Marin County was probably the most significant factor in their making the discovery.

That a previously uncollected new species, and one of potentially great significance in interpreting relationships within the genus, was discovered in such a botanically well known area suggests the need for a very careful look at any areas that are threatened by development or other disturbance, especially near expanding population centers. Had this species not been noticed soon, it might very well have become extinct without ever having been recorded.

In addition to those persons already mentioned I acknowledge with thanks the assistance of Dr. Rimo Bacigalupi and Dr. Lawrence R. Heckard in reviewing portions of the manuscript and translating the diagnostic description into Latin; Ms. Charlotte Mentges in preparing the illustration; other staff members of the University of California Herbarium and the University of California Botanical Garden in providing research space and time; and Dr. and Mrs. H. G. Baker in providing research materials and space.

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FLORISTIC RELATIONSHIPS OF ONION PEAK WITH SADDLE MOUNTAIN, CLATSOP COUNTY, OREGON

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Clatsop County occupies the northwestern tip of Oregon, bordered on the north by the Columbia River and on the west by the Pacific Ocean. It lies entirely within the Coast Range physiographic province, which in Oregon is a forested region divided between the coastal *Picea sitchensis* zone and the adjacent *Tsuga heterophylla* zone of vegetation (Franklin and Dyrness, 1969). In the geographical center of Clatsop County rises a three-humped, bald, rocky prominence known as Saddle Mountain, 1000 m in elevation and one of the highest peaks in the northern Oregon Coast Range. The flora of this mountain is of particular interest because of the disjunct occurrence here of a number of species from the Olympic Mountains, the Washington and Oregon Cascades, the Columbia River Gorge, and the high Coast Range peaks to the south (Detling, 1954). Saddle Mountain is presently considered to be the southern limit of distribution of several taxa in the Coast Range, including *Cladothamnus pyrolaeiflorus*, *Dodecatheon pulchellum*, *Anemone multifida*, *Douglasia laevigata*, *Erigeron peregrinus* ssp. *peregrinus*, *Lewisia columbiana* var. *rupicola*, *Synthyris schizantha*, and *Prenanthes alata*. Two taxa are assumed to be endemic to this peak: *Cardamine pattersonii* and *Saxifraga occidentalis* var. *latipetiolata*.

While Saddle Mountain is easily reached by road and trail, there are several other less accessible high peaks in Clatsop County that might be expected to have a similar flora. These mountains form an almost straight northeast-southwest diagonal across the county, reaching the ocean just south of the Tillamook County line. The map in Figure 1 shows all the areas above 762 m elevation and the principal named peaks. The geology of these highlands is similar, with rocky pinnacles, cliffs, and ridges formed by deeply weathered basalt breccias of Miocene volcanic intrusives that penetrate the surrounding early Tertiary sediments (Schlicker et al., 1972). These bare rocky summits stand above a continuous blanket of forest and support a varied herbaceous and shrubby flora of species adapted to cliffs, ravines, talus, and forest-border habitats. The boreal elements in this flora are probably favored by the cold, stormy winters and the protection from high summer temperatures afforded by shaded north slopes, seepage moisture, and especially by frequent summer fogs off the nearby ocean (Detling, 1954).

Recent logging operations on private land around Onion Peak, 24 km southwest of Saddle Mountain and 934 m in elevation, now allow easy

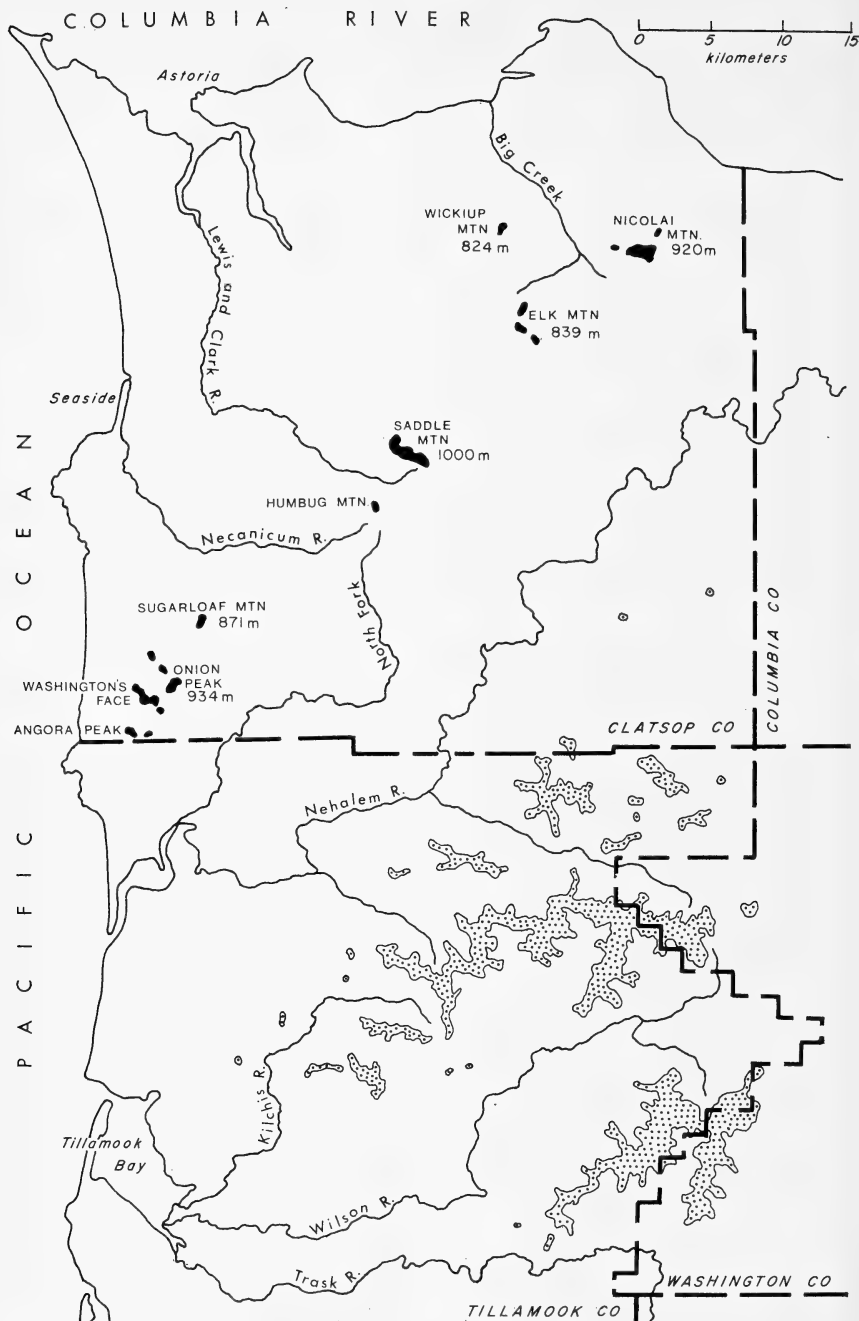


FIG. 1. Map of Clatsop County, Oregon, and parts of adjacent counties. Areas over 762 m elevation are shown in black for Clatsop County and are stippled for Tillamook and Washington Counties.

access to this, the second highest point in Clatsop County. In 1971 and 1972 I made four collecting trips to Onion Peak; the resulting specimens are deposited at Oregon State University and are the basis for the list of species given in this report. The first botanical exploration of Onion Peak was on July 7, 1967, by Dr. L. R. Heckard, who has very kindly allowed me to include his collections (now deposited in OSC and UC) in this report. I have not heard of any other plant collections from this mountain. While it is hoped the present plant list is relatively complete, one must admit that there are inaccessible cliffs and much rugged topography in the vicinity of Onion Peak, so that further additions to the list can be expected from future exploration.

DESCRIPTION OF ONION PEAK

Onion Peak is the highest point on a series of knobby ridges that include Washington's Face and Angora Peak. The north and west faces of these ridges mostly form precipitous cliffs, with deep weathering along vertical joints in the basalt. Onion Peak is an approximately conical monolith, whose blocky north and west slopes were once forested from base to summit, but whose south and east faces are massive slopes of bare rock. From a base at 730 m elevation, these smooth cliffs rise steeply for 120–150 m and then slope somewhat more gently to the summit. In the top 30–60 m, where the slope is only 30° – 40° , there is an area about two acres in extent on which extensive patches of thin soil occur, supporting a fairly rich flora of grasses, forbs, and cryptogams. This small "bald" is a miniature of the similar but much larger areas on Saddle Mountain, which were included in a survey of Coast Range "balds" by Aldrich (1972). The open summit area on Onion Peak gives way abruptly on the north and west sides to a forest of *Abies amabilis* and *Tsuga heterophylla*, with only a narrow shrub border of *Cladothamnus pyrolaeiflorus* and *Acer circinatum*. No grassy balds were observed on the adjacent high ridges of Washington's Face or Angora Peak; however, Sugarloaf Mountain, 5.2 km to the north and 871 m high, appears (through binoculars) to have a small bald on its summit.

The "forest" on the upper north and west sides of Onion Peak is a pitiful remnant of a few hundred trees, left after clear-cutting of all the surrounding area during the period of 1960–1965. The trees removed during these logging operations were principally *Thuja plicata*, *Abies* sp. (probably *Abies amabilis* for the most part, though perhaps some *A. procera*), and *Tsuga heterophylla*; smaller stands of old-growth *Pseudotsuga menziesii* occurred on some of the slopes, while the forests of *Picea sitchensis* at lower elevations to the west had mostly been logged earlier in the century (Dennis Rittenback, pers. comm.). Small stands of uncut forest are left on Washington's Face and the northwest spur of Onion Peak, but the latter is now finally being harvested! The almost complete removal of forest from even the steepest hillsides and

ridge-tops exposes these highlands to severe erosion. The present vegetation on the clear-cuts is mainly *Rubus spectabilis*, and tree regeneration is scarcely evident.

RELATIONSHIPS OF THE FLORA

The grassy bald on Onion Peak is isolated from Saddle Mountain by about 22.5 km of intervening lower-elevation forest. In species composition, their floras have many similarities together with some interesting differences, as will be discussed below. The accompanying map (fig. 1) shows that to the southeast of Onion Peak, in Tillamook and Washington Counties, there are large areas of the Coast Range that exceed 762 m elevation. These mountains, which are at the upper reaches of the Kilchis, Wilson, and Trask Rivers, are within the infamous Tillamook Burn and were devastated by a series of wildfires beginning in 1933. Because the summits of these peaks have been very little visited by botanists, it is not known whether or not the distinctive elements on Onion Peak and Saddle Mountain occur there as well. For comparing the latter two floras, a revised list of 268 taxa for Saddle Mountain (Chambers, unpublished) was used, which differs from Detling's list (1954) by numerous corrections and additions.

The list of vascular plants for Onion Peak is limited to collections made above 730 m; it does not include weeds and adventives that have come in along logging roads or in the clear-cuts. A few of the species were not found on Onion Peak, but were on Washington's Face in a bit of remaining forest at 850 m elevation, about 1.2 km southwest of the peak. The abbreviation "SM" indicates that the species is known to occur on Saddle Mountain. If Clatsop County is either the southern limit or northern limit for a species, in the Coast Range, this is stated in the list. The great majority of species extend both north and south of Onion Peak, either in the Coast Range or the Cascades, or both. The following discussion will call attention to some notable features of the flora. Nomenclature is based principally on Hitchcock et al. (1955-1969).

LIST OF TAXA FROM ONION PEAK

ACERACEAE: *Acer circinatum* Pursh (SM); *A. glabrum* Torr. var. *douglasii* (Hook.) Dippel (SM).

ARALIACEAE: *Oplopanax horridum* (J. E. Smith) Miq. (SM).

BERBERIDACEAE: *Berberis aquifolium* Pursh (see discussion); *B. nervosa* Pursh (SM); *Vancouveria hexandra* (Hook.) Morr. & Dcne. (SM).

BETULACEAE: *Alnus sinuata* (Regel) Rydb. (SM).

CAPRIFOLIACEAE: *Sambucus racemosa* L. ssp. *pubens* (Michx.) House (SM).

CARYOPHYLLACEAE: *Arenaria macrophylla* Hook. (SM); *A. rubella* (Wallenb.) Smith (SM, see discussion); *Cerastium arvense* L.

(SM); *Stellaria crispa* Cham. & Schlecht. (SM).

COMPOSITAE: *Achillea millefolium* L. (SM); *Anaphalis margaritacea* (L.) Benth. & Hook. (SM); *Arnica latifolia* Bong. (SM); *Cirsium edule* Nutt. (SM); *Erigeron peregrinus* (Pursh) Greene ssp. *peregrinus* (SM, southern limit, see discussion); *Eriophyllum lanatum* (Pursh) Forbes (SM); *Hieracium albiflorum* Hook. (SM); *Prenanthes alata* (Hook.) Dietr. (SM, southern limit); *Senecio flettii* Wieg. (southern limit; see discussion).

CRASSULACEAE: *Sedum oreganum* Nutt. (SM); *S. spathulifolium* Hook. (SM).

CRUCIFERAE: *Cardamine pattersonii* Hend. (SM, endemic; see discussion); *Erysimum asperum* (Nutt.) DC. (SM).

CUPRESSACEAE: *Thuja plicata* D. Don (SM).

CYPERACEAE: *Carex mertensii* Bong. (SM).

ERICACEAE: *Cladothamnus pyrolaeiflorus* Bong. (SM, southern limit); *Gaultheria shallon* Pursh (SM); *Menziesia ferruginea* Smith (SM); *Pyrola picta* Smith; *P. uniflora* L. (SM); *Vaccinium ovalifolium* Smith (SM); *V. parvifolium* Smith (SM).

FUMARIACEAE: *Dicentra formosa* (Andr.) Walp. (SM).

GRAMINEAE: *Agrostis diegoensis* Vasey (SM); *A. exarata* Trin. spp. *minor* (Hook.) C. L. Hitchc. (SM); *Bromus vulgaris* (Hook.) Shear var. *eximius* Shear; *B. vulgaris* var. *vulgaris* (SM); *Calamagrostis nutkaensis* (Presl) Steud. (SM); *Danthonia californica* Boland. (see discussion); *Deschampsia elongata* (Hook.) Benth. (SM); *Elymus glaucus* Buckl. (SM); *E. hirsutus* Presl (SM); *Festuca rubra* L. (SM, see discussion); *Glyceria elata* (Nash) M. E. Jones; *Koeleria nitida* Nutt. (SM; = *K. cristata* Pers., an illegitimate name); *Melica subulata* (Griseb.) Scribn. (SM); *Phleum alpinum* L. (SM); *Poa gracillima* Vasey (SM); *P. marcida* A. S. Hitchc. (SM); *Trisetum cernuum* Trin. (SM).

HYDROPHYLLACEAE: *Hydrophyllum tenuipes* Heller (SM); *Romanzoffia sitchensis* Bong. (SM).

IRIDACEAE: *Iris tenax* Dougl. ex Lindl. (SM); *Sisyrinchium bermudianum* L. (SM).

JUNCACEAE: *Luzula campestris* (L.) DC. (SM); *L. divaricata* Wats. (SM; = *L. parviflora* ssp. *fastigiata* (E. Mey.) Hamet-Ahti); *L. parviflora* (Ehrh.) Desv. (SM).

LABIATAE: *Prunella vulgaris* L. (SM); *Stachys mexicana* Benth. (SM).

LEGUMINOSAE: *Lotus micranthus* Benth. (SM).

LILIACEAE: *Allium cernuum* Roth (SM); *A. crenulatum* Wieg. (SM); *Camassia quamash* (Pursh) Greene var. *maxima* (Gould) C. L. Hitchc. (see discussion); *Clintonia uniflora* (Schult.) Kunth (SM); *Disporum smithii* (Hook.) Piper (SM); *Erythronium revolutum* Smith (SM); *Lilium columbianum* Hanson (SM); *Maianthemum dilatatum*

(Wood) Nels. & Macbr. (SM); *Scoliopus hallii* Wats.; *Smilacina racemosa* (L.) Desf. (SM); *S. stellata* (L.) Desf. (SM); *Stenanthium occidentale* Gray (SM); *Streptopus amplexifolius* (L.) DC. (SM); *S. roseus* Michx. (SM); *Trillium ovatum* Pursh (SM).

LYCOPODIACEAE: *Lycopodium clavatum* L. (SM).

ONAGRACEAE: *Epilobium alpinum* L. var. *lactiflorum* (Hausskn.) C. L. Hitchc. (SM); *E. angustifolium* L. (SM); *E. glandulosum* Lehm.; *E. minutum* Hook. (SM); *E. watsonii* Barbey (SM).

ORCHIDACEAE: *Corallorhiza mertensiana* Bong. (SM); *Habenaria saccata* Greene (see discussion); *Listera cordata* (L.) R. Br. (see discussion).

OXALIDACEAE: *Oxalis oregana* Nutt. (SM).

PINACEAE: *Abies amabilis* (Dougl.) Forbes (SM, see discussion); *Picea sitchensis* (Bong.) Carr. (SM); *Tsuga heterophylla* (Raf.) Sarg. (SM).

POLEMONIACEAE: *Microsteris gracilis* (Hook.) Greene (SM); *Phlox diffusa* Benth. ssp. *longistylis* Wherry (SM).

POLYGONACEAE: *Polygonum nuttallii* Small (SM).

POLYPODIACEAE: *Adiantum pedatum* L. (SM); *Athyrium filix-femina* (L.) Roth ssp. *cyclosorum* (Rupr.) C. Chr.; *Blechnum spicant* (L.) With. (SM); *Cryptogramma crispa* (L.) R. Br. var. *acrostichoides* (R. Br.) Clarke (SM); *Cystopteris fragilis* (L.) Bernh. (SM); *Dryopteris austriaca* (Jacq.) Woynar (SM); *Polypodium glycyrrhiza* D. C. Eaton (SM, see discussion); *Polystichum munitum* (Kaulf.) Presl (SM).

PORTULACACEAE: *Claytonia sibirica* L. (SM); *Lewisia columbiana* (Gray) Robins. var. *rupicola* (English) C. L. Hitchc. (SM, southern limit); *Montia parvifolia* (Moc.) Greene var. *flagellaris* (Bong.) C. L. Hitchc. (SM).

PRIMULACEAE: *Dodecatheon pulchellum* (Raf.) Merrill (SM, see discussion); *Trientalis latifolia* Hook. (SM).

RANUNCULACEAE: *Actaea rubra* (Ait.) Willd. (SM); *Coptis laciniata* Gray; *Delphinium menziesii* DC. var. *pyramidale* (Ewan) C. L. Hitchc. (SM); *Ranunculus uncinatus* D. Don var. *parviflorus* (Torr.) Benson (SM); *Trautvetteria caroliniensis* (Walt.) Vail var. *occidentalis* (Gray) C. L. Hitchc.

RIBESACEAE: *Ribes lacustre* (Pers.) Poir. (SM).

ROSACEAE: *Aruncus sylvestris* Kostel. (SM); *Filipendula occidentalis* (Wats.) How. (northern limit, see discussion); *Fragaria vesca* L. (SM); *F. virginiana* Duchesne var. *platypetala* (Rydb.) Hall (SM); *Rosa gymnocarpa* Nutt. (SM); *R. nutkana* Presl (SM); *Rubus pedatus* J. E. Smith (SM); *R. spectabilis* Pursh (SM); *R. ursinus* Cham. & Schlecht. (SM).

RUBIACEAE: *Galium triflorum* Michx. (SM).

SAXIFRAGACEAE: *Boykinia elata* (Nutt.) Greene (SM); *Heuchera*

micrantha Lindl. var. *diversifolia* (Rydb.) R. B. & L. (SM); *Saxifraga bronchialis* L. var. *vespertina* (Small) Rosend. (SM); *S. caespitosa* L. var. *emarginata* (Small) Rosend. (southern limit, see discussion); *S. ferruginea* Grah. var. *macounii* Engl. & Irmsch. (SM); *S. mertensiana* Bong. (SM); *S. oregana* How. (SM); *Tellima grandiflora* (Pursh) Dougl. (SM); *Tiarella trifoliata* L. (SM); *Tolmiea menziesii* (Pursh) T. & G. (SM).

SCROPHULARIACEAE: *Castilleja hispida* Benth. (SM); *C.* sp. (endemic ?, see discussion); *Collinsia parviflora* Lindl. (SM); *Mimulus dentatus* Nutt. ex Benth. (SM); *Nothochelone nemorosus* (Dougl. ex Lindl.) Straw (SM); *Orthocarpus pusillus* Benth. (SM); *Penstemon cardwellii* How. (SM, northern limit, see discussion); *P. serrulatus* Smith (SM); *Synthyris schizantha* (SM, southern limit).

SELAGINELLACEAE: *Selaginella oregana* D. C. Eaton (SM); *S. wallacei* Hieron. (SM).

TAXACEAE: *Taxus brevifolia* Nutt.

UMBELLIFERAE: *Conioselinum chinense* (L.) B. S. P. (SM, see discussion); *Heracleum sphondylium* L. (SM; = *H. lanatum* Michx.); *Lomatium martindalei* C. & R. var. *flavum* (G. N. Jones) Cronq. (SM); *Osmorhiza purpurea* (C. & R.) Suksd. (SM).

VALERIANACEAE: *Valeriana scouleri* Rydb. (SM).

VIOLACEAE: *Viola adunca* Smith (SM); *V. glabella* Nutt. (SM).

Berberis aquifolium, although widely distributed, has not yet been found on Saddle Mountain. On Onion Peak it occurs as dwarfed individuals at the junction of the bald area with the *Cladothamnus* shrub border.

Arenaria rubella is a questionable taxonomic entity in this part of Oregon. Seedlings transplanted from Onion Peak in 1972 flowered the first year and have continued to grow vegetatively since then (they survived subfreezing weather outdoors in Corvallis). The plants of Onion Peak and Saddle Mountain appear to be identical with those of the Queen Charlotte Islands that Calder and Taylor (1968) referred to *Arenaria stricta* Michx. ssp. *macra* (Nels. & Macbr.) Maguire. They are matted and strongly perennial, and thus do not fit *A. stricta* as defined by Hitchcock (Hitchcock et al., Part 2, 1964).

Erigeron peregrinus is represented on Onion Peak by a small but somewhat variable population that is best referred to ssp. *peregrinus*. The rays are white and the phyllaries vary from villous and eglandular to ciliate and dorsally glandular. The Saddle Mountain population is also variable; its rays range from white to violet, and its phyllaries are mostly ciliate with some dorsal glandular puberulence. On Saddle Mountain it grows sympatrically with *E. aliceae* Howell, which is absent from Onion Peak.

Senecio flettii was an unexpected discovery on Onion Peak; it is a

species of the Olympic Mountains and Washington Cascades and has never been found on Saddle Mountain or elsewhere in Oregon. The identification has been confirmed by Dr. T. M. Barkley.

Cardamine pattersonii is one of the rarest of Oregon's endemic species. It was known previously only from its type locality, Saddle Mountain, where it is quite abundant. On the summit bald of Onion Peak, it grows mainly on moss mats over bare rock, together with other ephemerals like *Orthocarpus pusillus*, *Lotus micranthus*, *Epilobium minutum*, *Microsteris gracilis*, and *Collinsia parviflora*. Although annual in its arid natural habitat, *C. pattersonii* will perennate when moisture is available throughout the summer. This was suspected by Hitchcock (Hitchcock et al., Part 2, 1964) and has been verified in potted transplants from Onion Peak, which formed new, vigorous rosettes from the base of the stem after fruiting and were not killed by freezing temperatures during the winter of 1972-1973.

Danthonia californica unexpectedly has not yet been found on Saddle Mountain, although the grassy bald areas there are much more extensive and varied than on Onion Peak.

Festuca rubra is common in the grassy area of both peaks. The report by Detling (1954) of *F. howellii* Hack. ex Beal (a synonym of *F. viridula* Vas.) on Saddle Mountain is probably based on the specimen *Ift* 85 (OSC), which is *F. rubra* misidentified as *F. howellii*.

Camassia quamash is abundant and very conspicuous in the deeper patches of soil on the Onion Peak bald. It could hardly have been overlooked on Saddle Mountain, so its absence there, although unexplained, is probably significant.

Habenaria saccata and *Listera cordata* are no doubt to be expected on or near Saddle Mountain, but I have seen no collections. Both *H. unalascensis* (Spreng.) Wats. and *H. greenii* Jeps. are common on Saddle Mountain, and *L. caurina* Piper has been found there. Proving the non-occurrence of particular orchid species, and also of various pyroloid and monotropoid Ericaceae, is difficult. *Chimaphila menziesii* (R. Br.) Spreng. ought to be found on both peaks, but has not been verified on either; *Monotropa uniflora* L. was found on Saddle Mountain but not Onion Peak.

Abies amabilis is the only fir in the forest remnants of Onion Peak and Washington's Face; on Saddle Mountain, however, *A. procera* Rehd. is common and *A. amabilis* is apparently rare. Another interesting conifer reported from Saddle Mountain is *Chamaecyparis nootkatensis* (D. Don) Spach, although I personally have not seen it there nor on Onion Peak.

Polypodium glycyrrhiza is the only species of this genus on Onion Peak, whereas on Saddle Mountain it occurs sympatrically with *P. montense* F. Lang.

The *Dodecatheon* found on Onion Peak and Saddle Mountain is

difficult to identify with assurance. Because of its dark connective and short, dark, free filaments, as well as its broad leaves that taper abruptly into the petiole, it superficially resembles *D. jeffreyi* Van Houtte of the type found in the Queen Charlotte Islands and southeast Alaska (e.g. *Jaques* 1500, Prince of Wales Island, OSC). However, the connective is smooth, the stigma is not very much enlarged, and the herbage is glabrous on some plants (although lightly glandular on others). Thompson (1953) specifically discussed the Saddle Mountain population and concluded it could be connected with *D. pulchellum* (*D. radicum* Greene of his treatment) through intermediates in the Columbia River gorge. Since I have no new evidence to offer, I am following Thompson's judgment.

Filipendula occidentalis is a rarely collected Oregon endemic, whose range is now known to extend north to Clatsop County and south to Lincoln County (*Henderson s.n.*, Aug. 4, 1928, Upper Siletz River; ORE). It has not yet been found on Saddle Mountain.

The population of *Saxifraga caespitosa* on Onion Peak better matches var. *emarginata*, of the Olympic Mountains and northward, than var. *subgemmifera* (Engl. & Irmsch.) C. L. Hitchc., found on adjacent Saddle Mountain. The differences are subtle ones of habit and leaf pubescence (Hitchcock et al., Part 3, 1961).

There is an apparently undescribed taxon of *Castilleja*, currently under study by Dr. Noel Holmgren, which was found on Onion Peak but has been searched for without success on Saddle Mountain. It somewhat resembles *C. parviflora* Bong. var. *oreopola* (Greenm.) Ownbey, but has corollas about 32 mm long.

Penstemon cardwellii reaches its northern limit in the Coast Range on Saddle Mountain. Detling's (1954) report of *P. menziesii* Hook. from there probably was based on *Patterson* 92 (at ORE), which proves to be *P. cardwellii* instead.

Conioselinum chinense has been confused with *Ligusticum apiifolium* (Nutt.) Gray; the latter was listed from Saddle Mountain (Detling, 1954) but this appears to be an error based on the specimen *Ifft* 136 (OSC), which is *C. chinense* initially misidentified as *Ligusticum*.

SUMMARY

The grassy bald atop Onion Peak is very much smaller than that on Saddle Mountain, but the two share many characteristic species. A partial listing of these is: *Arenaria rubella*, *Cerastium arvense*, *Erigeron peregrinus*, *Cardamine pattersonii*, *Cladanthamnus pyrolaeiflorus*, *Poa gracillima*, *Allium crenulatum*, *Phlox diffusa* ssp. *longistylis*, *Lewisia columbiana* var. *rupicola*, *Dodecatheon pulchellum*, *Saxifraga bronchialis* var. *vespertina*, *S. ferruginea* var. *macounii*, *Penstemon cardwellii*, and *Lomatium martindalei* var. *flavum*.

Plants found on Onion Peak but not on Saddle Mountain include:

Berberis aquifolium, *Senecio flettii*, *Danthonia californica*, *Camassia quamash*, *Saxifraga caespitosa* var. *emarginata*, and *Castilleja* sp.

Many species that occur on the open summits of Saddle Mountain are missing from Onion Peak. Selected examples of this group are: *Cryptantha intermedia* (Gray) Greene, *Campanula rotundifolia* L., *Silene douglasii* Hook., *Erigeron aliciae* How., *Agoseris aurantiaca* (Hook.) Greene, *Rudbeckia occidentalis* Nutt., *Senecio macounii* Greene, *Arabis hirsuta* (L.) Scop., *Poa sandbergii* Vas., *Phacelia nemoralis* Greene, *Trifolium longipes* Nutt., *T. microdon* H. & A., *T. microcephalum* Pursh, *Lloydia serotina* (L.) Sweet, *Erythronium grandiflorum* Pursh, *Sidalcea hirtipes* C. L. Hitchc., *Clarkia amoena* (Lehm.) Nels. & Macbr., *Collomia heterophylla* Hook., *Polygonum bistortoides* Pursh, *Douglasia laevigata* Gray, *Anemone multifida* Poir., *Thalictrum occidentale* Gray, *Geum triflorum* Pursh, *Potentilla gracilis* Hook., *Lithophragma parviflora* (Hook.) T. & G., *Saxifraga occidentalis* Wats., *Rhinanthus cristagalli* L., *Sanicula graveolens* DC., *Perideridia gairdneri* (H. & A.) Mathias, and *Plectritis congesta* (Lindl.) DC.

Many of the boreal elements in the flora of Saddle Mountain, as defined by Detling (1954), are now known to be present as well at the summit of Onion Peak. Since the latter is only 6.4 km from the ocean, it may differ climatically from the former, which is 11.3 km farther inland. In sum, however, the flora of Onion Peak is a generous sampling of Saddle Mountain with a few added novelties.

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ANNOTATED CHECK-LIST OF VASCULAR PLANTS
OF SAGEHEN CREEK DRAINAGE BASIN,
NEVADA COUNTY, CALIFORNIA

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Subsequent to the establishment of the University of California's Sagehen Creek Field Station in 1951, the Sagehen Creek Drainage Basin has been the site of numerous research projects. These research projects have yielded more than 50 scientific publications (Leopold, 1971). However, only two of these papers—a study of bogs (Rae, 1970) and a study of conifer regeneration following burns (Bock and Bock, 1969)—have been concerned with vegetation, the bulk of the investigations having been directed towards studies of animals. The lack of an inventory of vascular plants has severely hampered efforts to obtain a broader understanding of the relationships of plants and animals in this region. The present check-list, therefore, is an attempt to compile an annotated catalogue of vascular plants that will be useful in future research and teaching activities at the Sagehen Creek Field Station and in other localities of the northern Sierra Nevada in which there are similar environmental conditions.

The Sagehen Creek Drainage Basin is located in northeastern Nevada County, California, and is here defined as the roughly oval shaped upper Sagehen Creek valley, extending westerly from the point at which California State Highway 89 crosses Sagehen Creek to Carpenter Ridge (fig. 1); it is approximately 8.9 km long and averages about 4.8 km in width. Thus, the area comprising the Sagehen Creek Drainage Basin lies between meridians $120^{\circ} 12'$ and $120^{\circ} 20'$ west longitude and between parallels $39^{\circ} 24'$ and $39^{\circ} 27'$ north latitude. The elevation of this area ranges from 1874 m at State Highway 89 to approximately 2680 m at the summit of Carpenter Ridge.

Various studies of the geology of this region, including those of Axelrod (1962), Birkeland (1963, 1964), and Lindgren (1897) have revealed that the bed-rock is granodiorite of Jurassic or Cretaceous age. The bed-rock is overlain by andesite, the parent soil material, of Pliocene or Miocene age, with glacial moraine interspersed with Pleistocene alluvium. Glacial moraine occurs along Sagehen Creek from its headwaters almost to the Field Station and north to Independence Lake. Pleistocene alluvium occurs along the creek in a 3.2 km long strip, approximately 1.6 km upstream from the Field Station, and, together with stream terraces, downstream from the Field Station to the confluence of Sagehen Creek with the Little Truckee River. The ridges comprising the north bound-

ary of Sagehen Creek Drainage Basin consist primarily of andesite with occasional outcroppings of a coarse basaltic rock, olivine-diorite (Lindgren, 1897); however, the Sagehen Hills, which represent the southern boundary, are composed of andesite devoid of these outcroppings.

The climate is characterized by dry, warm summers with occasional thunder showers and by winters with heavy snowfalls. Since water derived from rain and heavy snowfall penetrates the porous volcanic rocks and collects on the impervious bed-rock, numerous springs of superficial origin are present. The largest springs occur at the bases of andesitic hills where, at ground level, the volcanic rocks and bed-rock come in contact. This spring water, from slightly acidic soils, is mainly a dilute solution of bicarbonates of calcium, magnesium, and sodium and generally has pH values in the range of 7.2 to 7.8. Due to the origin of the water, spring-fed streamlets contributing to the creek are characterized by a constant flow of water of rather low temperatures (Johnson and Needham, 1966).

The drainage basin is administered by the Tahoe National Forest and the disturbance of native vegetation is limited to grazing by sheep and to recreational activities of man during the summer. Thus, the vegetation is less disturbed than in adjacent valleys.

In general, the habitats present in the area include the wet banks of Sagehen Creek and its streamlet tributaries, "hanging" bogs, and moist meadows at lower elevations and dry, rocky meadows at higher elevations interspersed among mixed coniferous forest associations. These forest associations range from lodgepole-Jeffrey pine associations at lower elevations to red fir-western white pine associations at higher elevations. The principal landmarks are shown in Figure 1.

The following catalogue of plants has been compiled over the last seven years, primarily from the collections of the staff and students at the Sagehen Creek Field Station, and does not purport to be complete, as is indicated by the appended list of observations. Nevertheless, the specimens deposited in the Sagehen Creek Field Station Herbarium represent 438 taxa. These specimens include members of 349 species and 89 infra-specific taxa, representing 60 families and 217 genera. With few exceptions, nomenclature follows that of Munz (1959) and the arrangement of plant families is alphabetical.

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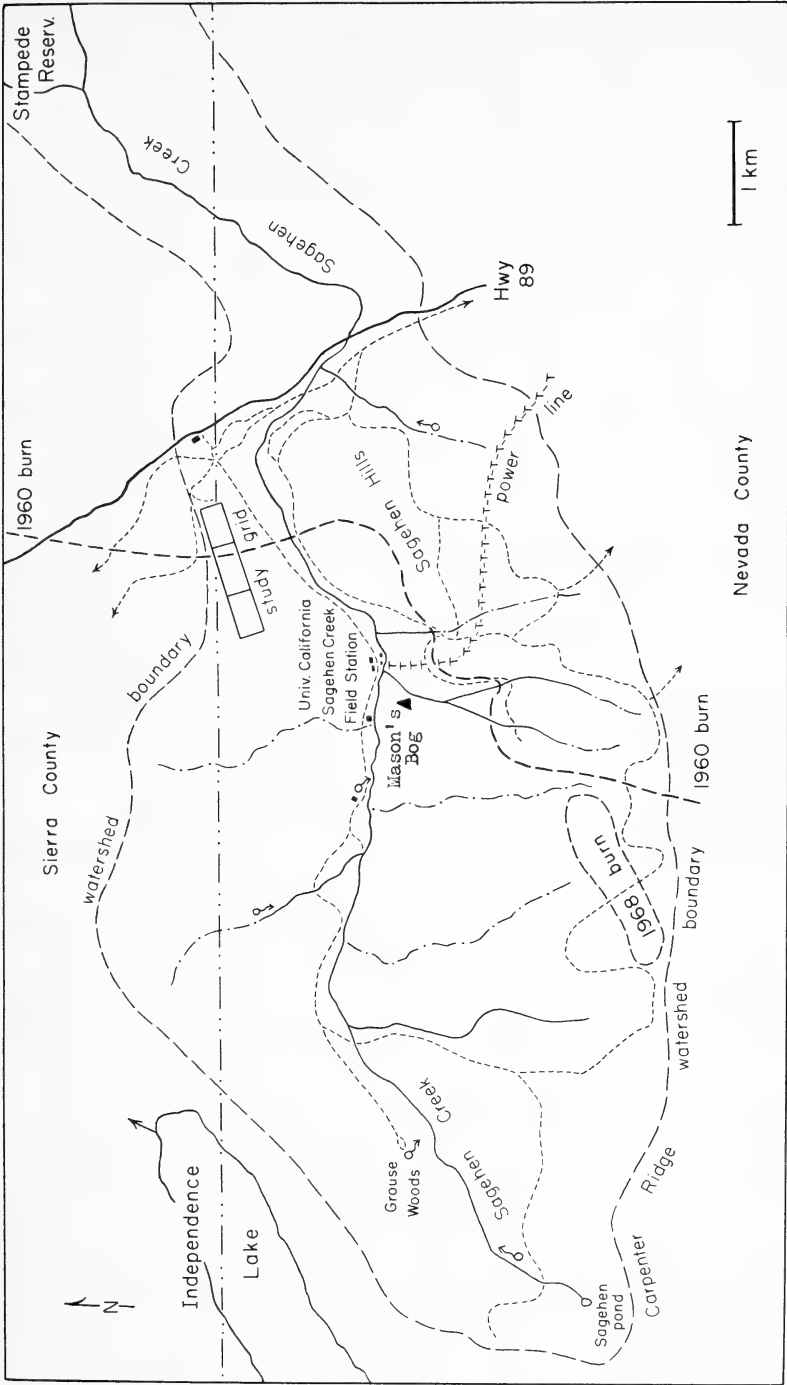


FIG. 1. Principal landmarks of the Sagehen Creek Drainage Basin.

CATALOGUE OF PLANTS

AMARYLLIDACEAE. Amaryllis Family

- Allium bisceptrum* Wats. Patis Onion. Infrequent; meadows and dry slopes.
A. campanulatum Wats. Sierra Onion. Common; dry slopes and open areas in woods.
A. validum Wats. Swamp Onion. Frequent; bogs and marshy areas near streamlets.
Brodiaea gracilis Wats. Slender Brodiaea. Frequent; dry open slopes.
B. hyacinthina (Lindl.) Baker. White Brodiaea. Frequent; dry open areas.
B. lutea (Lindl.) Mort. var. *analina* (Greene) Munz. Golden Brodiaea, Pretty Face. Infrequent; dry meadows and open areas in woods.

APOCYNACEAE. Dogbane Family

- Apocynum pumilum* (Gray) Greene. Mountain Dogbane. Frequent; exposed rocky slopes.

ASCLEPIADACEAE. Milkweed Family

- Asclepias fascicularis* Dcne. Narrow-leaved Milkweed. Rare; exposed rocky slopes.

ASPIDIACEAE. Shield Fern Family

- Cystopteris fragilis* (L.) Bernh. Brittle Fern. Infrequent; moist soil of headwaters of Sagehen Creek.

BETULACEAE. Birch Family

- Alnus tenuifolia* Nutt. Mountain Alder, Thin-leaved Alder. Frequent; along Sagehen Creek.

BORAGINACEAE. Borage Family

- Cryptantha affinis* (Gray) Greene. Common Cryptantha. Common; dry slopes and in woods.
C. simulans Greene. Pine Cryptantha. Infrequent; dry slopes and open places in woods.
Cynoglossum occidentale Gray. Western Hound's Tongue. Frequent; open places in woods.
Hackelia californica (Gray) Jtn. California Stickseed. Infrequent; gravelly slopes and open places in woods.
H. floribunda (Lehm.) Jtn. Many-flowered Stickseed. Frequent; shaded slopes and edges of woods.
H. micrantha (Eastw.) J. L. Gentry. Little-flowered Stickseed. Infrequent; moist shaded slopes in woods.

Plagiobothrys hispidulus (Greene) Jtn. Harsh Plagiobothrys. Frequent; moist meadows.

P. hispidus Gray. Bristly Popcorn Flower. Infrequent; dry gravelly slopes.

P. tener (Greene) Jtn. Slender Allocarya. Infrequent; moist lower meadows.

CAPRIFOLIACEAE. Honeysuckle Family

Lonicera cauriana Fern. Blue Fly Honeysuckle. Rare; moist shaded banks of Sagehen Creek at lower elevations.

L. conjugialis Kell. Double Honeysuckle. Rare; wooded slopes near Sagehen Creek.

L. involucrata (Richards.) Banks ex Spreng. Black Twin-berry. Infrequent; near bogs and edges of Sagehen Creek.

Sambucus caerulea Raf. Blue Elderberry. Infrequent; brushy slopes.

S. microbotrys Rydb. Mountain Red Elderberry. Infrequent; moist meadows on higher slopes.

Symphoricarpos acutus (Gray) Dieck. Sharp Snowberry. Infrequent; open rocky slopes.

S. vaccinioides Rydb. Mountain Snowberry. Infrequent; exposed rocky slopes.

CARYOPHYLLACEAE. Pink Family

Arenaria congesta Nutt. ex T. & G. Capitata Sandwort. Frequent; dry rocky slopes.

A. Kingii (Wats.) Jones var. *glabrescens* (Wats.) Maguire. King's Sandwort. Infrequent; Carpenter Ridge and higher rocky slopes.

A. Nuttallii Pax ssp. *gracilis* (Gray) Maguire. Nuttall's Slender Sandwort. Infrequent; higher rocky slopes and Carpenter Ridge.

Cerastium vulgatum L. Larger Mouse-ear Chickweed. Frequent; moist meadows.

Sagina saginoides (L.) Karst. var. *hesperia* Fern. Arctic Pearlwort. Infrequent; moist meadows.

Silene Douglasii Hook. Douglas's Campion. Frequent; dry rocky areas on lower slopes.

S. invisa Hitchc. & Maguire. Unseen Campion. Infrequent; higher meadows and Carpenter Ridge.

S. Menziesii Hook. Menzies's Campion. Infrequent; dry rocky areas on lower slopes.

S. montana Wats. Mountain Campion. Infrequent; dry rocky areas on lower slopes.

Spergularia rubra (L.) J. & C. Presl. Purple Sand Spurry. Rare; in disturbed areas.

Stellaria calycantha (Ledeb.) Bong. ssp. *interior* Hult. Interior Starwort. Infrequent; moist meadows.

S. longipes Goldie. Long-stalked Starwort. Frequent; moist meadows.

CHENOPODIACEAE. Goosefoot Family

Chenopodium album L. Pigweed, Lamb's Quarters. Infrequent; disturbed areas.

C. Berlandieri Moq. var. *Zschackei* (Murr.) Murr. Zschack's Pitseed Goosefoot. Rare; disturbed areas near Field Station.

C. incognitum H. A. Wahl. Disguised *Chenopodium*. Infrequent; disturbed areas near Sagehen Creek.

Monolepis Nuttalliana (Schult.) Greene. Nuttall's *Monolepis*. Infrequent; dry areas on lower slopes.

COMPOSITAE. Sunflower Family

Achillea lanulosa Nutt. Yarrow. Abundant; meadows and slopes in woods.

Antennaria rosea Greene. Rosy Everlasting. Frequent; meadows and shaded places in woods.

Arnica Chamissonis Less. ssp. *foliosa* (Nutt.) Maguire. Leafy Meadow Arnica. Frequent; moist meadows and near springs and streamlets.

A. discoidea Benth. var. *alata* (Rydb.) Cronq. Winged Rayless Arnica. Common; open places in woods and near Sagehen Creek.

Artemisia tridentata Nutt. Basin Sagebrush. Common; exposed slopes and edges of woods.

Aster adscendens Lindl. Long-leaved Aster. Infrequent; meadows.

A. alpigenus (T. & G.) Gray ssp. *Andersonii* (Gray) Onno. Anderson's Aster. Frequent; bogs and moist meadows.

A. integrifolius Nutt. Entire-leaved Aster. Infrequent; edges of dry meadows and in woods.

A. occidentalis (Nutt.) T. & G. Western Mountain Aster. Common; moist meadows and edges of woods.

Balsamorhiza sagittata (Pursh) Nutt. Arrow-leaved Balsamroot. Infrequent; meads and exposed slopes.

Chaenactis Douglasii (Hook.) H. & A. Hoary *Chaenactis*. Frequent; exposed gravelly slopes.

Cirsium Andersonii (Gray) Petr. Anderson's Thistle. Infrequent; exposed gravelly slopes.

C. Coulteri Harv. & Gray. Coulter's Thistle. Infrequent; exposed rocky slopes.

C. Drummondii T. & G. var. *acaulescens* (Gray) Macbr. Dwarf Thistle. Common; meadows and shaded places in woods.

Crepis intermedia Gray. Intermediate Hawksbeard. Infrequent; dry slopes and meadows.

Erigeron Coulteri Porter. Coulter's Daisy. Frequent; moist meadows and near Sagehen Creek.

E. peregrinus (Pursh) Greene ssp. *callianthemus* (Greene) Cronq. var. *angustifolius* (Gray) Cronq. Wandering Daisy. Infrequent; meadows.

Eriophyllum lanatum (Pursh) Forbes var. *integrifolium* (Hook.) Smiley.

- Entire-leaved *Eriophyllum*. Frequent; dry rocky slopes and open places in woods.
- Eupatorium occidentale* Hook. Western Eupatorium. Infrequent; rocky slopes and drying meadows.
- Gnaphalium palustre* Nutt. Lowland Cudweed. Frequent; damp meadows.
- G. thermale* Nels. Slender Cudweed. Infrequent; meadows.
- Haplopappus Bloomeri* Gray. Bloomer's Haplopappus. Infrequent; rocky slopes along edges of woods.
- Helianthella californica* Gray var. *nevadensis* (Greene) Jeps. Sierra Helianthella. Infrequent; meadows and dry slopes.
- Hieracium albiflorum* Hook. White-flowered Hawkweed. Frequent; meadows and edges of woods.
- Madia glomerata* Hook. Mountain Tarweed. Common; meadows and open places in woods.
- M. minima* (Gray) Keck. Least Tarweed. Infrequent; dry gravelly slopes in woods.
- Microseris nutans* (Hook.) Sch.-Bip. Nodding Scorzonella. Frequent; rocky slopes in woods.
- Psilocarphus brevissimus* Nutt. var. *brevissimus*. Dwarf Woolly-heads. Infrequent; drying lower meadows.
- Senecio integerrimus* Nutt. var. *exaltatus* (Nutt.) Cronq. Single-stemmed Butterweed. Common; meadows and dry slopes in woods.
- S. pauciflorus* Pursh. Rayless Alpine Butterweed. Frequent; moist areas in meadows and woods.
- S. pauciflorus* Pursh var. *jucundulus* Jeps. Streambank Butterweed. Infrequent; wet meadows and along banks of Sagehen Creek.
- S. triangularis* Hook. Arrowhead Butterweed. Frequent; moist meadows and banks of streamlets.
- Solidago canadensis* L. ssp. *elongata* (Nutt.) Keck. Meadow Goldenrod. Infrequent; moist meadows and shaded places in woods.
- Stephanomeria lactucina* Gray. Large-flowered Stephanomeria. Infrequent; open sandy places in woods on lower slopes.
- Taraxacum officinale* Weber. Common Dandelion. Common; meadows and moist places in woods.
- Tragopogon dubius* Scop. Yellow Salsify. Frequent; disturbed areas near Field Station and along roads.
- Wyethia mollis* Gray. Mountain Mule-ears. Common; dry meadows and exposed slopes in woods.

CONVOLVULACEAE. Morning-Glory Family

- Convolvulus arvensis* L. Bindweed. Rare; disturbed areas along roads.

CORNACEAE. Dogwood Family

- Cornus stolonifera* Michx. American Dogwood. Rare; edge of Sagehen Creek.

CRUCIFERAE. Mustard Family

- Arabis glabra* (L.) Bernh. Tower-Mustard. Frequent; dry open areas of lower slopes.
- A. Holboellii* Hornem. var. *pinetorum* (Tides.) Roll. Holboell's Rock-
cress. Frequent; dry open areas on lower slopes.
- A. Holboellii* Hornem. var. *retrofracta* (Grah.) Rydb. Infrequent; dry
rocky areas on lower slopes.
- A. Lyallii* Wats. Lyall's Rock-cress. Infrequent; gravelly soils of
Carpenter Ridge and higher slopes.
- A. platysperma* Gray. Broad-seeded Rock-cress. Infrequent; higher
dry slopes and Carpenter Ridge.
- Barbarea orthoceras* Ledeb. American Winter-cress. Frequent; moist
meadows.
- Capsella Bursa-pastoris* (L.) Medic. Shepherd's-Purse. Infrequent; dis-
turbed areas near Field Station.
- Cardamine Breweri* Wats. Brewer's Bitter-cress. Frequent; bogs and
along streamlets.
- Descurania Richardsonii* (Sweet) O. E. Schulz ssp. *incisa* (Engelm.)
Detl. Infrequent; disturbed areas on lower slopes.
- D. Richardsonii* (Sweet) O. E. Schulz ssp. *viscosa* (Rydb.) Detl.
Mountain Tansy-mustard. Infrequent; moist shaded areas on lower
slopes.
- Draba stenoloba* Ledeb. var. *nana* (O. E. Schulz) C. L. Hitchc. Alaska
Whitlow-grass. Infrequent; moist meadows and along streamlets.
- D. stenoloba* Ledeb. var. *ramosa* C. L. Hitchc. Infrequent; shaded
areas and in woods.
- Erysimum perenne* (Wats. ex Cov.) Abrams. Sierra Wallflower. Infre-
quent; disturbed areas and open rocky places.
- Ledipidum virginicum* L. var. *pubescens* (Greene) C. L. Hitchc. Downy
Pepper-grass. Infrequent; dry open areas.
- Nasturtium microphyllum* Boenn. ex Rchb. Small-leaved Water-cress.
Infrequent; along streamlets.
- N. officinale* R. Br. Water-cress. Frequent; in running water of small
streamlets.
- Raphanus sativus* L. Wild Radish. Infrequent; disturbed areas near Field
Station.
- Rorippa curvisiliqua* (Hook.) Bessey. Western Yellow-cress. Frequent;
moist meadows.
- Sisymbrium altissimum* L. Tumble-Mustard. Infrequent; disturbed areas
along roads.
- Streptanthus tortuosus* Kell. Mountain Streptanthus. Infrequent; dis-
turbed areas on lower dry slopes.
- Thlaspi arvense* L. Field Penny-cress. Rare; meadows near Field Station.

CUPRESSACEAE. Cypress Family

- Calocedrus decurrens* (Torr.) Florin. Incense-cedar. Rare; higher dry

slopes.

Juniperus occidentalis Hook. Western Juniper. Very rare; dry slopes.

CUSCUTACEAE. Dodder Family.

Cuscuta californica Choisy. California Dodder. Infrequent; meadows.

CYPERACEAE. Sedge Family

Carex aquatilis Wahl. Water Sedge. Common; bogs and edges of Sagehen Creek.

C. arctogena H. Sm. Water Sedge. Common; bogs and edges of Sagehen Creek.

C. athrostachya Olney. Slender-beaked Sedge. Frequent; wet meadows.

C. aurea Nutt. Golden-fruited Sedge. Infrequent; boggy areas and edges of streamlets.

C. capitata L. Capitata Sedge. Frequent; damp meadows and along streamlets in woods.

C. Cusickii Mkze. Cusick's Sedge. Common; marshy areas and edges of streamlets.

C. disperma Dewey. Soft-leaved Sedge. Infrequent; in woods along streamlets.

C. Douglasii W. Boott. Douglas's Sedge. Abundant; open, dry meadows.

C. eurycarpa Holm. Well-fruited Sedge. Common; bogs and damp meadows.

C. heteroneura W. Boott. Various-nerved Sedge. Frequent; dry soils in woods.

C. integra Mkze. Smooth-beaked Sedge. Infrequent; damp meadows.

C. Jonesii Bailey. Jones's Sedge. Common; meadows.

C. Kelloggii W. Boott. Kellogg's Sedge. Common; bogs and adjacent to streamlets in meadows.

C. lanuginosa Michx. Woolly Sedge. Common; wet meadows.

C. limosa L. Shore Sedge. Frequent; bogs.

C. multicostata Mkze. Many-ribbed Sedge. Common; damp meadows.

C. rostrata Stokes. Beaked Sedge. Infrequent; wet meadows.

C. simulata Mkze. Short-beaked Sedge. Abundant; bogs and damp meadows.

C. teneraeformis Mkze. Sierra Slender Sedge. Infrequent; marshy areas.

C. vernacula Bailey. Vernacular Sedge, Native Sedge. Frequent; bogs.

C. vesicaria L. Inflated Sedge. Common; bogs and damp meadows.

C. Whitneyi Olney. Whitney's Sedge. Infrequent; wet meadows.

Eriophorum gracile Koch. Slender Cotton-grass. Abundant; bogs.

Heleocharis quinqueflora (Hartm.) Schwarz. Five-flowered Spike-rush. Frequent; bogs.

Scirpus microcarpus Presl. Small-fruited Bulrush. Infrequent; damp meadows.

DROSERACEAE. Sundew Family

Drosera anglica Huds. Oblong-leaved Sundew. Common; bogs.

D. rotundifolia L. Round-leaved Sundew. Common; bogs.

EQUISETACEAE. Horstail Family.

Equisetum arvense L. Common Horsetail. Frequent; along Sagehen Creek and streamlet tributaries.

E. laevigatum A. Br. Braun's Scouring-rush. Common; bogs and streamlets.

ERICACEAE. Heath Family

Arctostaphylos nevadensis Gray. Pinemat Manzanita. Frequent; exposed slopes and in woods.

A. patula Greene. Green-leaved Manzanita. Common; exposed slopes and in woods.

Sarcodes sanguinea Torr. Snow Plant. Infrequent; rocky slopes in woods.

Vaccinium occidentale Gray. Western Blueberry, Western Huckleberry. Frequent; edges of bogs.

EUPHORBIACEAE. Spurge Family

Euphorbia serpyllifolia Pers. Thyme-leaved Spurge. Rare; disturbed areas along roads.

FAGACEAE. Beech Family

Castanopsis sempervirens (Kell.) Dudl. Bush Chinquapin, Sierra Chinquapin. Infrequent; among mixed conifers on middle and upper slopes.

Quercus vaccinifolia Kell. Huckleberry Oak. Infrequent; among mixed conifers on open rocky slopes.

FUMARIACEAE. Fumitory Family

Dicentra uniflora Kell. Steer's Head. Infrequent; gravelly soil of Carpenter Ridge and higher slopes.

GENTIANACEAE. Gentian Family

Gentiana Amarella L. Northern Gentian. Infrequent; banks of Sagehen Creek.

G. Newberryi Gray. Alpine Gentian. Infrequent; moist meadows and banks of Sagehen Creek.

G. simplex Gray. Hiker's Gentian. Frequent; moist meadows.

GRAMINEAE. Grass Family

Agropyron Parishii Scribn. & Sm. Parish's Wheat-grass. Frequent; dry slopes and meadows.

A. trachycaulum (Link) Malte. Slender Wheat-grass. Common; meadows.

- Agrostis exarata* Trin. Western Bent-grass. Common; meadows.
A. idahoensis Nash. Idaho Bent-grass. Common; meadows.
A. scabra Willd. Rough Hair-grass, Tickle-grass. Frequent; meadows.
Alopecurus aequalis Sobol. Little Meadow-foxtail. Infrequent; meadows.
Bromus ciliatus L. Fringed Brome. Frequent; dry soils at edges of meadows.
B. marginatus Nees. Large Mountain Brome-grass. Common; meadows and dry slopes.
B. Orcuttianus Vasey. Orcutt's Brome-grass. Frequent; dry soils.
B. tectorum L. Cheat Grass, Downy Cheat. Abundant; dry soils.
B. tectorum L. var. *glabratus* Spenner. Infrequent; dry slopes.
Dactylis glomerata L. Orchard Grass. Common; meadows.
Deschampsia caespitosa (L.) Beauv. Tufted Hair-grass. Common; meadows and damp soils.
D. danthonioides (Trin.) Munro ex Benth. Annual Hair-grass. Frequent; meadows.
D. elongata (Hook.) Munro ex Benth. Slender Hair-grass. Abundant; meadows and slopes.
Elymus cinereus Scribn. & Merr. Gray Rye-grass. Infrequent; meadows and dry slopes.
E. glaucus Buckl. Western Rye-grass. Frequent; dry soils.
E. triticoides Buckl. Alkali Rye-grass. Common; dry slopes.
Festuca rubra L. Red Fescue. Infrequent; meadows.
Glyceria elata (Nash) Hitchc. Tall Manna-grass. Infrequent; meadows.
G. pauciflora Presl. Few-flowered Manna-grass. Infrequent; meadows.
G. striata (Lam.) Hitchc. Fowl Meadow Grass. Frequent; meadows and damp soils.
Hordeum brachyantherum Nevskii. Meadow Barley. Frequent; meadows.
H. jubatum L. Foxtail. Common; dry slopes.
Melica bulbosa Geyer ex Porter & Coult. Western Melica. Infrequent; meadows and moist soils.
M. fugax Bol. var. *inexpansa* Suksd. Small Onion-grass. Rare; dry rocky soils.
M. fugax Bol. var. *Macbridei* (Rowland) Beetle. Rare; dry rocky soils.
M. stricta Bol. Nodding Melica. Infrequent; dry rocky slopes.
Muhlenbergia filiformis (Thurb.) Rydb. Slender Muhlenbergia. Frequent; bogs and damp meadows.
Oryzopsis hymenoides (R. & S.) Ricker. Sand Bunch Grass, Indian Mountain Rice. Infrequent; damp meadows.
Phleum alpinum L. Mountain Timothy. Frequent; meadows.
P. pratense L. Cultivated Timothy. Frequent; meadows and dry slopes.
Poa epilis Scribn. Mountain Bluegrass. Abundant; meadows.
P. nervosa (Hook.) Vasey. Hooker's Bluegrass. Infrequent; shaded slopes.

- P. nevadensis* Vasey ex Scribn. Nevada Bluegrass. Frequent; meadows and woods.
- P. Pringlei* Scribn. Pringle's Bluegrass. Infrequent; dry rocky slopes.
- P. Sandbergii* Vasey. Sandberg's Bluegrass. Infrequent; dry rocky slopes.
- P. scabrella* (Thurb.) Benth. ex Vasey. Malpais Bluegrass. Infrequent; dry soils.
- Sitanion Hystrix* (Nutt.) J. G. Sm. Bottlebrush Squirrel-tail. Frequent; meadows and dry slopes.
- Stipa Elmeri* Piper & Brodie ex Scribn. Elmer's Stipa. Infrequent; among mixed conifers on dry rocky slopes.

HYDROPHYLLACEAE. Waterleaf Family

- Hesperochiron pumilus* (Griseb.) Porter. Dwarf Hesperochiron. Rare; moist slopes and meadows.
- Hydrophyllum capitatum* Dougl. var. *alpinum* Wats. Alpine Woolen-breeches. Common; moist slopes and shaded places in woods.
- Nama Lobbii* Gray. Lobb's Nama. Infrequent; dry brushy areas previously burned.
- Nemophila parviflora* Dougl. ex Benth. var. *Austinae* (Eastw.) Brand. Austin's Small-flowered Nemophila. Infrequent; moist wooded areas on lower slopes.
- N. pedunculata* Dougl. ex Benth. Mountain Nemophila. Infrequent; moist wooded places on lower slopes.
- N. spatulata* Cov. Sierra Nemophila. Frequent; meadows and moist lower slopes.
- Phacelia hastata* Dougl. ex Lehm. Silver-leaf Phacelia. Common; dry rocky areas, (aff. *Phacelia mutabilis* Greene).
- P. humilis* T. & G. Low Phacelia. Common; dry gravelly slopes and edges of woods.
- P. hydrophylloides* Torr. ex Gray. Waterleaf Phacelia. Infrequent; gravelly slopes and open places in woods.

HYPERICACEAE. St. John's-wort Family

- Hypericum anagalloides* Cham. & Schlect. Tinker's Penny, Creeping St. John's-wort. Frequent; boggy areas and stream banks.
- H. formosum* HBK. var. *Scouleri* (Hook.) Coult. Scouler's St. John's-wort. Frequent; boggy areas and near springs.

IRIDACEAE. Iris Family

- Iris missouriensis* Nutt. Western Blue-flag. Frequent; dry meadows and open rocky areas in woods.
- Sisyrinchium idahoense* Bickn. Idaho Blue-eyed Grass. Infrequent; meadows and moist areas in woods.

JUNCACEAE. Rush Family

- Juncus balticus* Willd. var. *montanus* Engelm. Baltic Rush. Common; meadows and along streamlets in woods.
- J. chlorocephalus* Engelm. Green-headed Rush. Infrequent; meadows and moist lower slopes.
- J. dubius* Engelm. Mariposa Rush. Infrequent; damp meadows and stream banks.
- J. longistylus* Torr. Long-styled Rush. Infrequent; moist meadows and stream banks.
- J. nevadensis* Wats. Sierra Rush. Common; bogs and damp shadows.
- J. orthophyllus* Cov. Straight-leaved Rush. Frequent; bogs and damp meadows.
- Luzula campestris* (L.) DC. Common Wood-rush. Frequent; stream banks and adjacent to streamlets in bogs.
- L. divaricata* S. Wats. Forked Wood-rush. Frequent; bogs.

LABIATAE. Mint Family

- Mentha arvensis* L. Field Mint. Infrequent; along banks of Sagehen Creek at lower elevations.
- Monardella lanceolata* Gray. Mustang Mint. Infrequent; dry gravelly slopes.
- M. odoratissima* Benth. Mountain Monardella. Frequent; open rocky slopes and in woods.
- M. odoratissima* Benth. ssp. *pallida* (Heller) Epl. Pale Monardella. Common; exposed rocky slopes and in woods.
- Stachys rigida* Nutt. ex Benth. ssp. *rivularis* (Heller) Rpl. Brook Hedge Nettle. Frequent; moist open areas and along banks of Sagehen Creek.

LEGUMINOSAE. Pea Family

- Lotus crassifolius* (Benth.) Greene. Thick-leaved Lotus. Infrequent; dry areas on lower slopes.
- L. Purshianus* (Benth.) Clem. & Clem. Pursh's Lotus. Frequent; open rocky areas on lower slopes.
- Lupinus Andersonii* Wats. var. *apertus* (Heller) C. P. Sm. Anderson's Lupine. Infrequent; rocky slopes and edges of woods.
- L. arbustus* Dougl. ssp. *calcaratus* (Heller) D. Dunn. Douglas's Spurred Lupine. Infrequent; meadows and open slopes.
- L. arbustus* Dougl. ssp. *silvicola* (Heller) D. Dunn. Infrequent; lower dry rocky slopes in woods.
- L. Breweri* Gray. Brewer's Lupine. Infrequent; open rocky slopes and on burned areas.
- L. caudatus* Kell. Kellogg's Spurred Lupine. Infrequent; among mixed conifers on dry lower slopes.

- L. Lyallii* Gray. Lyall's Lupine. Infrequent; Carpenter Ridge and higher rocky slopes.
- L. polyphyllus* Lindl. ssp. *superbus* (Heller) Munz. Superb Lupine. Frequent; bogs and moist shaded places.
- Trifolium Andersonii* Gray. Anderson's Clover. Infrequent; dry open areas on lower slopes.
- T. longipes* Nutt. Long-stalked Clover. Frequent; meadows and moist shaded places.
- T. monanthum* Gray. Carpet Clover. Infrequent; near springs.
- T. productum* Greene. Shasta Clover. Frequent; moist meadows and shaded places.
- T. Wormskioldii* Lehm. Wormskiold's Clover. Infrequent; moist meadows.

LEMNACEAE. Duckweed Family

- Lemna minima* Phil. Least Duckweed. Frequent; slow moving streamlets.
- L. trisulca* L. Ivy-leaved Duckweed. Frequent; slow moving streamlets.

LENTIBULARIACEAE. Bladderwort Family

- Utricularia vulgaris* L. Common Bladderwort. Rare; open water in Mason's Bog.

LILIACEAE. Lily Family

- Calochortus Leichtlinii* Hook. f. Leichtlin's Mariposa. Frequent; dry open areas.
- Camassia Quamash* (Pursh) Greene ssp. *breviflora* Gould. Short-flowered Camass. Abundant; meadows.
- Fritillaria atropurpurea* Nutt. Purple Fritillary. Frequent; dry slopes and open places in woods.
- Lilium parvum* Kell. Small Tiger Lily. Infrequent; damp shaded areas near springs and in meadows.
- Smilacina stellata* (L.) Desf. Star-flower. Frequent; damp meadows and near streamlets.
- Tofieldia glutinosa* (Michx.) Pers. ssp. *occidentalis* (Wats.) C. L. Hitchc. Western Tofieldia. Frequent; bogs.
- Veratrum californicum* Durand. Corn-Lily, Skunk-Cabbage. Common; shaded places in damp meadows.
- Zigadenus paniculatus* (Nutt.) Wats. Sand-corn, Panicked Zygadene. Frequent; dry places in meadows and woods.

LIMNANTHACEAE. False Mermaid Family

- Floerkea proserpinacoides* Willd. False Mermaid. Rare; moist meadows at lower elevations.

LINACEAE. Flax Family

Linum perenne L. ssp. *Lewisii* (Pursh) Hult. Western Blue Flax. Infrequent; Carpenter Ridge and higher dry slopes and meadows.

LOASACEAE. Loasa Family

Mentzelia dispersa Wats. Nada Stick-leaf. Very rare; dry disturbed places near Field Station.

LORANTHACEAE. Mistletoe Family

Arceuthobium americanum Nutt. ex Engelm. American Dwarf Mistletoe. Infrequent; on *Pinus Murrayana* on lower slopes.

A. campylopodum Engelm. f. *abietinum* (Engelm.) Gill. Fir Dwarf Mistletoe. Infrequent; on *Abies magnifica* on higher slopes.

MALVACEAE. Mallow Family

Sidalcea glaucescens Greene. Glaucous Sidalcea. Infrequent; burned and open places on lower slopes.

S. oregana (Nutt.) Gray ssp. *spicata* (Regel) Greene. Spiked sidalcea. Common; moist meadows.

ONAGRACEAE. Evening-Primrose Family

Camissonia andina (Nutt.) Raven. Plateau Primrose. Infrequent; lower rocky slopes among sagebrush.

C. subacaulis (Pursh) Raven. Sun Cup. Common; meadows and open places in woods.

Epilobium angustifolium L. Fireweed. Infrequent; moist lower slopes and along Sagehen Creek.

E. brevistylum Barb. Slender Willow-herb. Frequent; moist meadows and bogs.

E. glaberrimum Barb. Glaucous Willow-herb. Infrequent; moist meadows and near streamlets.

E. Halleianum Hausskn. Hall's Willow-herb. Infrequent; along streamlets on higher slopes.

E. obcordatum Gray. Rock-fringe. Infrequent; higher slopes and Carpenter Ridge.

E. oregonense Hausskn. Oregon Willow-herb. Common; bogs and wet meadows near streamlets.

E. paniculatum Nutt. ex T. & G. Panicked Willow-herb. Rare; in disturbed places along roads.

E. Pringleanum Hausskn. Pringle's Willow-herb. Infrequent; moist areas and near springs.

Gayophytum diffusum T. & G. ssp. *parviflorum* Lewis & Szweykowski. Small-flowered Diffuse Gayophytum. Frequent; dry slopes and exposed places.

G. heterozygum Lewis & Szweykowski. Heterozygous Gayophytum. Infrequent; dry rocky places on lower slopes.

Ludwigia palustris (L.) Ell. American Marsh Purslane. Infrequent; bogs and wet meadows.

ORCHIDACEAE. Orchid Family

Corallorhiza maculata Raf. Spotted Coral-root. Rare; open places in woods above Mason's Bog.

Habenaria dilatata (Pursh) Hook. var. *leucostachys* (Lindl.) Ames. Sierra Rein-orchis, White-flowered Bog Orchid. Frequent; bogs and near springs.

H. sparsiflora Wats. Sparsely-flowered Bog Orchid. Infrequent; bogs and near springs.

Spiranthes Romanzoffiana Cham. & Schlecht. Hooded Ladies' Tresses. Common; bogs.

OROBANCHACEAE. Broom-rape Family

Orobanche uniflora L. Naked Broom-rape. Rare; on *Saxifraga* along streamlets in bogs.

O. uniflora L. var. *Sedi* (Suksd.) Achey. Rare; on *Artemisia* on dry lower slopes.

PAPAVERACEAE. Poppy Family

Eschscholzia californica Cham. California Poppy. Rare; disturbed places near Field Station.

PINACEAE. Pine Family

Abies concolor (Gord. & Glend.) Lindl. White Fir. Frequent; dry lower slopes.

A. magnifica A. Murr. Red Fir. Frequent; dry higher slopes.

Pinus jeffreyi Grev. & Balf. Jeffrey Pine. Common; dry lower slopes.

P. lambertiana Dougl. Sugar Pine. Infrequent; dry higher slopes.

P. monticola Dougl. Western White Pine. Frequent; dry higher slopes.

P. murrayana Grev. & Balf. Lodgepole Pine. Common; lower slopes and borders of meadows and bogs.

Tsuga mertensiana (Bong.) Carr. Mountain Hemlock. Frequent; dry higher slopes.

POLEMONIACEAE. Phlox Family

Collomia grandiflora Dougl. ex Lindl. Large-flowered Collomia. Frequent; open areas on rocky slopes.

C. linearis Nutt. Narrow-leaved Collomia. Frequent; meadows and open places.

C. tinctoria Kell. Yellow-staining Collomia. Infrequent; exposed rocky slopes.

Gilia capillaris Kell. Smooth-leaved Gilia. Frequent; dry slopes and meadows.

G. leptalea (Gray) Greene ssp. *bicolor* Mason & Grant. Two-colored

- Bridges's Gilia. Common; dry slopes and meadows.
- Ipomopsis aggregata* (Pursh) V. Grant. Scarlet Gilia, Skyrocket. Frequent; exposed slopes and edges of woods.
- Leptodactylon pungens* (Torr.) Rydb. ssp. *Hookeri* (Dougl.) Wherry. Hooker's Granite Gilia. Rare; exposed brushy slopes.
- Linanthus ciliatus* (Benth.) Greene. Whisker-brush, Bristly-leaved Linanthus. Common; dry rocky slopes and open places.
- L. ciliatus* (Benth.) Greene var. *neglectus* (Greene) Jeps. Frequent; dry rocky slopes.
- L. Harknessii* (Curran) Greene. Harkness's Linanthus. Frequent; exposed rocky slopes.
- L. Harknessii* (Curran) Greene ssp. *condensatus* Mason. Infrequent; dry meadows and slopes.
- Microsteris gracilis* (Dougl. ex Hook.) Greene. Slender Phlox. Frequent; meadows and open places in woods.
- M. gracilis* (Dougl. ex Hook.) Greene ssp. *humilis* (Greene) V. Grant. Infrequent; moist meadows.
- Navarretia Breweri* (Gray) Greene. Brewer's Navarretia. Infrequent; dry meadows.
- N. divaricata* (Torr.) Greene. Mountain Navarretia. Frequent; open exposed areas and dry places in woods.
- N. propinqua* Suksd. Great Basin Navarretia. Common; moist meadows.
- N. subuligera* Greene. Awl-leaved Navarretia. Infrequent; dry rocky slopes.
- Phlox diffusa* Benth. Spreading Phlox. Frequent; exposed rocky slopes and open places in woods.
- Polemonium californicum* Eastw. Low Polemonium. Infrequent; shaded places on higher slopes and Carpenter Ridge.
- P. caeruleum* L. ssp. *occidentale* (Greene) J. F. Davids. Western Polemonium. Common; wet meadows and near springs and stream banks.

POLYGONACEAE. Buckwheat Family

- Eriogonum marifolium* T. & G. Marum-leaved Eriogonum. Infrequent; Carpenter Ridge and higher dry slopes.
- E. nudum* Dougl. ex Benth. Naked-stemmed Eriogonum, Tibinagua. Frequent; dry open areas on lower slopes.
- E. spergulinum* Gray. Spurry Eriogonum. Infrequent; road beds and disturbed places on lower slopes.
- E. umbellatum* Torr. var. *umbellatum*. Sulphur Flower. Frequent; dry open slopes.
- Oxyria digyna* (L.) Hill. Mountain Sorrel. Infrequent; higher rocky slopes and Carpenter Ridge.
- Polygonum aviculare* L. Common Knotweed. Frequent; lower slopes and disturbed places.

- P. bistortoides* Pursh. Western Bistort, Snakeweed. Common to locally abundant; wet meadows.
- P. Davisiae* Brew. ex Gray. Davis's Knotweed. Infrequent; higher dry slopes and Carpenter Ridge.
- P. Douglasii* Greene. Douglas's Knotweed. Infrequent; dry lower slopes.
- P. Kelloggii* Greene. Kellogg's Knotweed. Infrequent; dry areas on lower slopes.
- P. minimum* Wats. Leafy Dwarf Knotweed. Infrequent; wet areas near Sagehen Creek.
- P. natans* (Michx.) Eaton. American Water Persicaria, Water Smartweed. Rare; springs and edges of Sagehen Creek.
- P. phytolaccaefolium* Meissn. Alpine Knotweed. Infrequent; dry brushy slopes.
- P. shastense* Brew. ex Gray. Shasta Knotweed. Infrequent; higher dry slopes and Carpenter Ridge.
- P. spergulariaeforme* Meissn. Fall Knotweed, Spurry Knotweed. Frequent; disturbed dry places.
- Rumex paucifolius* Nutt. ex Wats. Alpine Sheep Sorrel. Infrequent; higher slopes and Carpenter Ridge.
- R. salicifolius* Weinm. Willow Dock. Frequent; dry meadows and open places on lower slopes.
- R. triangulivalvis* (Danser) Rech. f. var. *oreolapathum* Rech. f. Infrequent; wet meadows.

PORTULACACEAE. Purslane Family

- Calandrinia ciliata* (R. & P.) DC. var. *Menziesii* (Hook.) Macbr. Red Maids. Common; dry meadows and open areas on lower slopes.
- Calyptridium umbellatum* (Torr.) Greene. Pussy Paws. Common; dry open areas.
- C. umbellatum* (Torr.) Greene var. *caudiciferum* (Gray) Jeps. Infrequent; higher dry slopes and Carpenter Ridge.
- Lewisia nevadensis* (Gray) Rob. Nevada Lewisia. Infrequent; lower slopes in woods.
- L. triphylla* (Wats.) Rob. Three-leaved Lewisia. Infrequent; higher meadows and slopes and Carpenter Ridge.
- Montia Chamissoi* (Ledeb.) Dur. & Jacks. Toad-lily. Common; moist meadows.
- M. perfoliata* (Donn) Howell var. *depressa* (Gray) Jeps. Depressed Miner's-Lettuce. Frequent; shaded places in woods.

PRIMULACEAE. Primrose Family

- Dodecatheon Jeffreyi* Van Houtte. Jeffrey's Shooting Star. Common; moist meadows and bogs.
- Primula suffrutescens* Gray. Sierra Primrose. Infrequent; higher dry slopes and Carpenter Ridge.

PTERIDACEAE. Bracken Family

Cheilanthes gracillima C. C. Eat. Lace Fern. Infrequent; rocky outcrops of lower dry slopes.

Pteridium aquilinum (L.) Kuhn var. *pubescens* Underw. Western Bracken. Common; south-facing slopes.

PYROLACEAE. Wintergreen Family

Allotropa virgata T. & G. ex Gray. Sugar Stick. Frequent; ridges in woods.

Chimaphila Menziesii (R. Br. ex D. Don) Spreng. Little Prince's Pine, Pipsissewa. Infrequent; shaded slopes in woods.

C. umbellata (L.) Barton var. *occidentalis* (Rydb.) Blake. Western Prince's Pine. Infrequent; dry brushy slopes.

Pteropora Andromedeae Nutt. Pinedrops. Frequent; shaded areas among pines.

Pyrola californica Krisa. Bog Wintergreen. Infrequent; edges of bogs.

P. picta Sm. White-veined Wintergreen, Shin-leaf. Infrequent; dry shaded areas among pines.

P. picta Sm. ssp. *dentata* (Sm.) Piper. Nootka Wintergreen. Common; lower dry slopes among pines.

RANUNCULACEAE. Crowfoot Family

Aconitum columbianum Nutt. Columbia Monkshood. Common; damp shaded places near Sagehen Creek.

Aquilegia formosa Fisch. var. *truncata* (F. & M.) Jones. Columbine. Frequent; moist shaded places in woods.

Caltha Howellii (Huth) Greene. White Marsh-marigold. Frequent; boggy places in woods.

Delphinium glaucum Wats. Glaucous Rocky Mountain Larkspur. Infrequent; higher wet meadows and Carpenter Ridge.

D. Nuttallianum Pritz. ex Walp. Nuttall's Larkspur. Common; bogs and moist meadows.

Myosurus aristatus Benth. ssp. *montanus* (Campbell) Stone. Sedge Mouse-tail. Frequent; bogs and pools near springs.

Paeonia Brownii Dougl. ex Hook. Western Peony. Frequent; lower rocky slopes.

Ranunculus alismaefolius Geyer ex Benth. var. *Hartwegii* (Greene) Jeps. Water-plantain Buttercup. Frequent; moist meadows.

R. alismaefolius Geyer ex Benth. var. *Lemmonii* (Gray) L. Benson. Infrequent; near springs.

R. aquatilis L. var. *capillaceus* (Thuill.) DC. Water Buttercup. Frequent; in Sagehen Creek and streamlet tributaries.

R. occidentalis Nutt. var. *Eisenii* (Kell.) Gray. Eisen's Western Buttercup. Frequent; moist meadows.

- R. occidentalis* Nutt. var. *ultramontanus* Greene. Infrequent; adjacent to streamlets in meadows.
- R. orthorhynchus* Hook. Straight-beaked Buttercup. Infrequent; in meadows.
- R. uncinatus* D. Don. Hooked Buttercup. Infrequent; moist semi-shaded places in edges of woods.
- Thalictrum Fendleri* Engelm. ex Gray. Fendler's Meadow-Rue. Common; moist shaded places in edges of woods.
- T. sparsiflorum* Turcz. Few-flowered Meadow-Rue. Frequent; moist shaded places near Sagehen Creek.

RHAMNACEAE. Buckthorn Family

- Ceanothus prostratus* Benth. Squaw Carpet, Mahala Mats. Common; open areas among pines on rocky slopes.
- C. velutinus* Dougl. ex Hook. Tobacco Brush. Common; burned areas and open places on wooded rocky slopes.
- Rhamnus alnifolia* L'Her. Alder-leaved Coffeeberry. Rare; near springs.

ROSACEAE. Rose Family

- Amelanchier pumila* Nutt. Smooth Service-berry. Frequent; partly shaded lower slopes.
- Cercocarpus ledifolius* Nutt. Curl-leaved Mountain-mahogany. Infrequent; higher dry rocky slopes and Carpenter Ridge.
- Fragaria virginiana* L. ssp. *platypetala* Staudt. Broad-petaled Strawberry. Frequent; moist shaded places in woods.
- Geum macrophyllum* Willd. Large-leaved Avens. Frequent; moist meadows and banks of Sagehen Creek.
- Holodiscus microphyllus* Rydb. Small-leaved Rock-spiraea. Infrequent; dry rocky slopes.
- Horkelia fusca* Lindl. ssp. *pseudocapitata* (Rydb.) Keck. False-headed Dusky Horkelia. Infrequent; open areas and edges of woods.
- Ivesia sericoleuca* (Rydb.) Rydb. Plumas Ivesia. Frequent; meadows and dry slopes.
- I. unguiculata* Gray. Yosemite Ivesia. Frequent; meadows and edges of woods.
- Potentilla glandulosa* Lindl. ssp. *nevadensis* (Wats.) Keck. Sierra Sticky Cinquefoil. Common; meadows and open places in woods.
- P. gracilis* Dougl. ex Hook. ssp. *Nuttallii* (Lehm.) Keck. Nuttall's Cinquefoil. Frequent; meadows and edges of woods.
- Prunus emarginata* (Dougl.) Walp. Bitter Cherry. Frequent; open rocky slopes.
- Purshia tridentata* (Pursh) DC. Northern Antelope Brush, Bitter-brush. Common; dry rocky slopes.
- Rosa californica* Cham. & Schlecht. California Rose. Frequent; moist shaded places among conifers on lower slopes.

- R. Woodsii* Lindl. var. *ultramontana* (Wats.) Jeps. Interior Rose. Frequent; moist areas and edges of woods on lower slopes.
Rubus parviflorus Nutt. Thimbleberry. Rare; near springs.
Spiraea densiflora Nutt. ex T. & G. Rose-colored Meadow-sweet. Infrequent; higher rocky slopes and Carpenter Ridge.

RUBIACEAE. Madder Family

- Galium bifolium* Wats. Low Mountain Bedstraw. Infrequent; in edges of woods and near disturbed places on lower slopes.
G. Grayanum Ehrend. Gray's Bedstraw. Infrequent; higher rocky slopes and Carpenter Ridge.
G. mexicanum HBK. var. *asperulum* (Gray) Dempster. Tall Rough Bedstraw. Infrequent; moist soils in woods and near Sagehen Creek.
G. trifidum L. var. *subbiflorum* Wieg. Trifid Bedstraw. Common; wet meadows and near Sagehen Creek.
G. triflorum Michx. Sweet-scented Bedstraw. Frequent; moist shaded places and near Sagehen Creek.
Kelloggia galioides Torr. Kelloggia. Frequent; dry shaded slopes in woods.

SALICACEAE. Willow Family

- Populus tremuloides* Michx. Quaking Aspen. Frequent; along Sagehen Creek and near springs.
P. trichocarpa T. & G. Black Cottonwood. Very rare; single tree on Sagehen Creek, ca. 4.8 km west of Field Station.
Salix argophylla Nutt. Silver-leaved Willow. Infrequent; moist meadows and near streamlets.
S. Geyeriana Anderss. Geyer's Willow. Common; along Sagehen Creek.
S. Geyeriana Anderss. var. *argentea* (Bebb) C. K. Schneid. Silver Geyer's Willow. Infrequent; along Sagehen Creek.
S. lasiandra Benth. Red Willow. Frequent; along Sagehen Creek.
S. lasiandra Benth. var. *lancifolia* (Anderss.) Bebb. Lance-leaved Red Willow. Infrequent; along Sagehen Creek.
S. Lemmonii Bebb. Lemmon's Willow. Common; along Sagehen Creek and near springs.

SAXIFRAGACEAE. Saxifrage Family

- Lithophragma glabrum* Nutt. Rock Star. Infrequent; moist shaded places in edges of woods.
Mitella Breweri Gray. Brewer's Miterwort. Infrequent; shaded places in edges of bogs.
Parnassia palustris L. var. *californica* Gray. California Grass-of-Parnassus. Infrequent; wet meadows.
Ribes cereum Dougl. White Squaw Currant. Frequent; dry exposed slopes.

- R. divaricatum* Dougl. var. *inermis* (Rydb.) McMinn. White-stemmed Gooseberry. Infrequent; moist shaded places on lower slopes.
R. montigenum McClat. Alpine Prickly Currant. Infrequent; dry places on higher slopes.
R. nevadense Kell. Sierra Nevada Currant. Infrequent; dry higher ridges and Carpenter Ridge.
R. Roezlii Regel. Sierra Gooseberry. Frequent; dry open slopes.
R. viscosissimum Pursh var. *Hallii* Jancz. Hall's Sticky Currant. Infrequent; moist shaded places and near springs.
Saxifraga oregana Howell. Bog Saxifrage. Common; bogs and moist meadows.
S. odontoloma Piper. Brook Saxifrage. Frequent; near streamlets in bogs and headwaters of Sagehen Creek.

SCROPHULARIACEAE. Figwort Family

- Castilleja Applegatei* Fern. Wavy-leaved Indian Paint-brush. Frequent; exposed dry rocky slopes.
C. miniata Dougl. ex Hook. Great Red Indian Paint-brush. Common; moist sandy areas near springs and Sagehen Creek.
C. nana Eastw. Dwarf Alpine Indian Paint-brush. Infrequent; exposed rocky places on higher slopes and Carpenter Ridge.
C. pilosa (Wats.) Rydb. Hairy Indian Paint-brush. Infrequent; gravelly slopes and edges of dry meadows.
Collinsia parviflora Dougl. ex Lindl. Small-flowered Blue-eyed Mary. Frequent; moist shaded places and near streamlets in meadows.
C. Torreyi Gray var. *Wrightii* (Wats.) Jtn. Wright's Blue-eyed Mary. Infrequent; exposed gravelly places on higher slopes.
Gratiola ebracteata Benth. Bractless Hedge-hyssop. Rare; disturbed places in lower wet meadows.
Mimulus Breweri (Greene) Cov. Brewer's Monkey-flower. Infrequent; drying meadows.
M. guttatus Fisch. ex DC. Common Large Monkey-flower. Common; bogs, wet meadows and banks of streamlets.
M. moschatus Dougl. ex Lindl. Musk Flower. Common; moist soil near springs and banks of streamlets.
M. primuloides Benth. Primrose Monkey-flower. Abundant; bogs and wet meadows.
M. rubellus Gray. Ciliolate-toothed Monkey-flower. Infrequent; sandy slopes near meadows.
M. Suksdorfii Gray. Suksdorf's Monkey-flower. Frequent; moist meadows.
M. Tilingii Regel. Larger Mountain Monkey-flower. Frequent; damp meadows and near streamlets.
M. Torreyi Gray. Torrey's Monkey-flower. Infrequent; partially shaded places in woods on lower slopes.

- Orthocarpus Copelandii* Eastw. var. *cryptanthus* (Piper) Keck. Infrequent; exposed dry slopes of higher ridges and Carpenter Ridge.
- O. hispidus* Benth. Hairy Orthocarpus. Common; meadows.
- Pedicularis attollens* Gray. Little Elephant's Head. Infrequent; moist areas of higher slopes and Carpenter Ridge.
- P. groenlandica* Retz. ssp. *surrecta* (Benth.) Piper. Raised Elephant's Head. Common; bogs, damp meadows and shaded places.
- P. semibarbata* Gray. Pine-woods Lousewort. Frequent; dry shaded slopes in woods.
- Penstemon deustus* Dougl. ex Lindl. Hot-rock Penstemon. Common; dry rocky slopes.
- P. gracilentus* Gray. Slender Penstemon. Common; dry rocky slopes and open places in woods.
- P. heterodoxus* Gray. Sierran Penstemon. Infrequent; higher dry slopes and Carpenter Ridge.
- P. laetus* Gray ssp. *Roetzlii* (Regel) Keck. Roetzl's Gay Penstemon. Frequent; rocky slopes in woods.
- P. Lemmonii* Gray. Bush Beard-tongue. Frequent; brushy rocky slopes.
- P. Newberryi* Gray. Mountain Pride. Infrequent; exposed higher rocky slopes and Carpenter Ridge.
- P. Rydbergii* A. Nels. Meadow Penstemon. Common; meadows.
- P. speciosus* Dougl. ex Lindl. Showy Penstemon. Frequent; exposed sandy slopes.
- P. speciosus* Dougl. ex Lindl. ssp. *Kennedyi* (A. Nels.) Keck. Kennedy's Penstemon. Infrequent; higher rocky slopes and Carpenter Ridge.
- Verbascum Thapsus* L. Common Mullein. Infrequent; brushy rocky slopes and near streamlets.
- Veronica americana* (Raf.) Schw. American Brooklime. Frequent; moist places and near banks of Sagehen Creek.
- V. peregrina* L. ssp. *xalapensis* (HBK.) Penn. Jalapa Speedwell. Infrequent; moist meadows.
- V. serpyllifolia* L. var. *humifusa* (Dickson) Vahl. Low Thyme-leaved Speedwell. Common; banks of streamlets and moist places in woods.

SOLANACEAE. Nightshade Family

- Chamaesaracha nana* (Gray) Gray. Dwarf Chamaesaracha. Frequent; dry exposed sandy places.

UMBELLIFERAE. Carrot Family

- Angelica Breweri* Gray. Brewer's Angelica. Infrequent; exposed rocky slopes.
- Heracleum lanatum* Michx. Cow-parsnip. Infrequent; moist slopes and shaded places.

- Ligusticum Grayi* Coult. & Rose. Gray's Lovage. Frequent; moist slopes and areas along Sagehen Creek.
- Lomatium dissectum* (Nutt.) Math. & Const. Fern-leaved Lomatium. Infrequent; in edges of woods on rocky lower slopes.
- Osmorhiza chilensis* H. & A. Mountain Sweet-cicely. Infrequent; moist shaded places along streamlets.
- O. occidentalis* (Nutt.) Torr. Western Sweet-cicely. Frequent; woods and shaded places along Sagehen Creek.
- Perideridia Bolanderi* (Gray) Nels. & Macbr. Bolander's Yampah. Frequent; meadows and exposed slopes.
- P. Lemmonii* (Coult. & Rose) Chuang & Const. Lemmon's Yampah. Infrequent; meadows and exposed slopes at edges of woods.
- Pteryxia terebinthina* (Hook.) Coult. & Rose var. *californica* (Coult. & Rose) Math. California Pteryxia. Carpenter Ridge and high exposed ridges.
- Sanicula graveolens* Poepp. ex DC. Sierra Sanicle. Rare; open woods near streamlets.
- Sphenosciadium capitellatum* Gray. Ranger's Button, Swamp Whiteheads. Common; near springs and along Sagehen Creek.

VALERIANACEAE. Valerian Family

- Valeriana capitata* Pall. ex Link ssp. *californica* (Heller) F. G. Meyer. California Valerian. Frequent; moist meadows, streamlet banks, and shaded places in woods.

VIOLACEAE. Violet Family

- Viola adunca*. Sm. Western Dog Violet. Infrequent; moist slopes.
- V. Macloskeyi* Lloyd. Macloskey's Violet. Frequent; moist places in woods and along banks of Sagehen Creek.
- V. purpurea* Kell. ssp. *integrifolia* Baker & Clausen. Frequent; exposed slopes and edges of woods.
- V. purpurea* Kell. ssp. *mesophyta* Baker & Clausen. Infrequent; dry slopes and edges of woods.

PLANTS REPORTEDLY OBSERVED IN THE SAGEHEN CREEK DRAINAGE BASIN BUT NOT COLLECTED

- Agoseris glauca* (Pursh) Greene var. *laciniata* (D. C. Eat.) Smiley.
- Aquilegia formosa* Fisch. var. *pauciflora* (Greene) Boothman.
- Arabis Davidsonii* Greene.
- Arnica cordifolia* Hook.
- Artemisia Douglasiana* Bess.
- A. ludoviciana* Nutt. ssp. *incompta* (Nutt.) Keck.
- Calochortus Nuttallii* Torr.
- Calycadenia mollis* Gray.
- Carex filifolia* Nutt.

- Chrysothamnus viscidiflorus* (Hook.) Nutt. ssp. *pumilus* (Nutt.) Hall & Clem.
Cryptantha pterocarya (Torr.) Greene.
C. Torreyana (Gray) Greene.
Dodecatheon alpinum (Gray) Greene.
Epilobium anagallidifolium Lam.
E. exaltatum E. Drew.
Gayophytum ramosissimum T. & G.
Helenium Hoopesii Gray.
Ivesia Gordonii (Hook.) T. & G.
Juncus macrandrus Cov.
Lemna gibba L.
Lupinus meionanthus Gray.
L. sellulus Kell.
Matricaria matricarioides (Less.) Porter.
Perideridia Gairdneri (H. & A.) Math.
Phacelia curvipes Torr. ex Wats.
P. heterophylla Pursh ssp. *virgata* (Greene) Heckard.
Pinus ponderosa Dougl. ex P. C. Lawson.
Poa Hansenii Scribn.
Prunus virginiana L. var. *demissa* (Nutt.) Torr.
Quercus chrysolepis Liebm. var. *nana* (Jeps.) Jeps.
Salix lutea Nutt.
Sambucus melanocarpa Gray.
Scirpus criniger Gray.
Silene Lemmonii Wats.
Stachys albens Gray.
Trifolium cyathiferum Lindl.
Veronica arvensis L.

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PROSTRATENESS IN ACACIA FARNESIANA FROM THE WESTERN COAST OF MEXICO UNDER UNIFORM ENVIRONMENTAL CONDITIONS

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Acacia farnesiana (L.) Willd. populations in Sinaloa, Mexico, have diverse stem orientation. Those on sandy beaches along Mazatlan Bay are extremely prostrate. Though not continuous in distribution, plants in clay soils 4.8 km. east of the dunes have upright stems typical of populations in Mexico and Texas. To determine if stem orientation was a local modification in a beach habitat by otherwise upright plants, collections from various beach and inland sites were compared under uniform conditions in central Texas.

Beaches were visited in Nayarit (San Blas), Sonora (Guaymas), and Colima (Manzanillo), but *A. farnesiana* was not observed in sandy habitats similar to those of populations along the Sinaloa coast. Although upright plants of *Acacia* are widely distributed, the prostrate forms may be restricted to Sinaloa.

Morphologically the *A. farnesiana* populations of Mexico differ from those of the Caribbean. As shown by Peacock and McMillan (1968) the Caribbean plants have larger leaves than those of Mexico and Texas when grown under controlled environmental conditions. McMillan and Cope (1969) showed that the widespread distribution in South America, Africa, Hawaii, and Europe is of the Caribbean type. Isely (1969) has referred the Caribbean type to *A. farnesiana* and the Texas-Mexico type to *A. smallii* Isely. The populations in Mexico west of Sierra Madre Occidental have pods that are longer and more slender than those of populations east of the mountain range and probably represent a local form of this widespread *A. farnesiana* complex.

MATERIALS AND METHODS

Scarified seeds were germinated on moist filter paper in petri dishes. The collections represented mixed seed from three plants except those from Altata. The two collections at Altata were from individual plants. Collection sites are cited in Table 1.

One week from sowing the seedlings were individually planted in 23 cm clay pots of fine sandy loam and were placed in a growth chamber with 15-hr light periods and 30° C day and 24° C night temperatures. The seedlings were in the growth chambers for 45 days and were subsequently in the greenhouse over-winter. The plants were transferred to out-of-doors conditions from April to November.

TABLE 1. PROSTRATENESS IN ACACIA FARNESIANA FROM WESTERN MEXICO UNDER UNIFORM ENVIRONMENTAL CONDITIONS

Collection site	Prostrate index (stem fraction \times angle)	SD	Mean total stem length (cm)	Mean basal stem section (cm)	Percentage of total stem	Angles of basal stem section ($^{\circ}$)
Beach						
1. Mazatlan-A	77.5	9.3	74.3	13.8	18.6	77.1
2. La Cruz	62.4	3.4	72.0	17.6	24.4	76.0
3. Altata-A	60.6	14.0	40.7	11.3	27.8	75.0
Altata-B	54.5	9.1	61.7	15.4	25.0	65.5
Average	63.8		62.2	14.5	24.0	73.4
Inland						
4. Culiacan	38.5	19.9	37.9	14.9	39.3	88.0
5. Esquinapa	36.4	6.9	60.8	24.3	40.0	88.7
6. Mazatlan-B	21.4	8.8	45.1	24.0	53.2	90.0
7. Los Mochis	14.5	5.6	38.1	22.5	59.1	87.5
Average	27.7		45.4	21.4	47.9	88.6

Measurements were recorded on ten one-year-old plants for each collection. The length of each stem segment or branch was measured and its fraction of the total stem calculated. The angle of a segment was calculated by drawing a straight line from the tip to the base of that segment and giving its departure from vertical. Each fraction was multiplied by its angle and the results summed as a prostrate index. A completely upright plant would have an index of 0° and a totally prostrate plant an index of 90° . The length of the basal stem portion and its angle of orientation are given in Table 1 with the indices of prostrateness.

RESULTS

The three beach populations, Mazatlan-A, La Cruz, and Altata (—A, —B), had the greatest indices of prostrateness (Table 1). The Mazatlan-A plants showed the greatest total stem growth and the lowest percentage of stem as a basal straight portion. Although La Cruz and Altata plants were more similar to Mazatlan-A plants than to those of inland populations they were intermediate between Mazatlan-A and Culiacan populations.

The average prostrate index for the four beach collections was 63.8 and for the four inland collections was 27.7. The distinctness of the two groups is affected, however, by the large standard deviation of the Culiacan collection. This Culiacan material suggests prostrate tendencies within inland plants.

The initial stem elongation for all four inland collections was more upright, $87.5\text{--}90.0^\circ$, than that of the beach collections, $65.5\text{--}77.1^\circ$. The plants of Altata-B showed the greatest tendency for stems to develop initially away from the vertical and those of the upright population, Mazatlan-B, had the greatest tendency for initial vertical orientation.

The Mazatlan collections show a strong contrast in prostrateness (fig. 1). Mazatlan-A from the beach with a prostrate index of 77.5 and Mazatlan-B from an inland site with an index of 21.4 nearly span the total range of index values. Because the distribution at Mazatlan is not continuous, it was not possible to determine if a gradient of prostrateness occurs in one region.

DISCUSSION

Populations of *A. farnesiana* from western Mexico showed diverse stem orientation under the same environmental conditions. Whereas all of the plants produced branches at diverse angles, those of the sandy beach habitats showed the greatest tendency for the branches to depart from the vertical. Plants grown from seed collected in inland sites showed a selection toward more upright stem production.

The prostrateness of the experimental populations correlated with the prostrateness of the parent plants. The plants grown from seed collected on the Mazatlan beach showed the greatest prostrate index and the



FIG. 1. Comparison of plants from Mazatlan, Sinaloa. The plants are from seed collected in the beach population (1,2) and in the population on clay soils 4.8 km east of the beach (3,4).

plants in the beach ecosystem were the most prostrate of those examined in Sinaloa. The experimental plants from Altata were the least prostrate of the beach populations. At Altata, the plants were not on fore-dune habitats as at the other two beach sites and were the least prostrate of the beach populations.

Hannon and McMillan (1972) compared plants from the Mazatlan beach with plants of Saltillo, Coahuila, and demonstrated that prostrate-ness was modified by interaction with light intensity. Beach plants were much more upright under low light intensities but inland plants were only slightly modified by various conditions of light intensity, temperature, and photoperiod. The greater niche plasticity of the beach population offers selective advantage in instable coastal ecosystems. The ability to produce upright stems in low light intensity provides competitive advantage in the dense growth of a subtropical beach ecosystem and the production of prostrate stems under higher light intensities results in sand dunes with a protective cover of thorny stems.

ACKNOWLEDGMENTS

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NOTES AND NEWS

A LECTOTYPE FOR THE HINDS WALNUT.—Jepson wrote about the Hinds walnut at least seven times between 1908 and 1923, either as *Juglans californica* Watson var. *Hindsii* Jepson (Bull. S. Calif. Acad. Sci. 7:23,24. 1908; Flora of California 1:365. 1909; Trees of California, p. 145, 1909; Silva of California, Memoirs Univ. Calif. 2:195. 1910) or as *J. Hindsii* Jepson (Madroño 1:55-57. 1917; Trees of California, second edition, pp. 109, 215. 1923; Manual of the flowering plants of California, p. 279. 1923), but at no time did he cite a collection. Moreover, no collection, either in the Jepson Herbarium or in the University of California Herbarium, has been indicated as the type. Since there continues to be some doubt as to the precise taxonomic status that should be accorded the Hinds walnut (cf. Munz, P.A., 1959, A California flora, p. 909) as well as to the interpretation of its floristic position (cf. Thomsen, H.H., Madroño 17:1-10. 1963), it is desirable and important that a lectotype be designated.

The following specimen has been selected to typify this walnut: *W. L. Jepson No. 2189*, collected May 3, 1903, on the east slope of the Napa Range near Wooden Valley, Napa County; JEPS 58696. This collection was known to Jepson throughout the years when he was concerned with the tree, and it came from one of the localities listed by him when he diagnosed the plant both in English and Latin (Jepson, W. L. 1909. Flora of California 1:365). The locality was also cited by Ralph E. Smith (Univ. Calif. Agr. Exp. Sta. Bull. 203:27, 1909) in whose account of the native California walnuts the specific name was first published and who described the locality even as recently as 1949 (Pacific Disc. 2(6):14).

At this time, when designating a specimen to typify the Hinds walnut, it is appropriate to review the proper author designation for the specific name that has been variously given as Jepson, (Jepson) Jepson, Rehder, (Jepson) Rehder, and Jepson ex R. E. Smith. The last, as it is given by both Rehder (Rehder, A. 1949. Bibliography of cultivated trees and shrubs hardy in the cooler temperate regions of the northern hemisphere, p. 128) and by Little (Little, Jr., E. L. 1953. Check list of native and naturalized trees of the United States (including Alaska). Agricultural Handbook No. 41, p. 214), is the correct author designation. Although the publication of the varietal name in January, 1908, preceded by nearly two years the publication of the specific name in November, 1909, Smith makes no allusion to the varietal name in his paper. The first use of the specific name by Jepson himself (Madroño 1:56, 1917) was simply *Juglans Hindsii* Jepson—but it is well-known that Jepson employed parenthetical authorship erratically.

I am grateful to Dr. L. R. Heckard, Curator of the Jepson Herbarium, for help in the selection of this type.—JOHN THOMAS HOWELL, Department of Botany, California Academy of Sciences, San Francisco 94118.

"BARK STRIPING" IN *ARCTOSTAPHYLOS* (ERICACEAE)

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A conspicuous characteristic of certain species of *Arctostaphylos* is the development of decorticated areas of varying size on their twigs, branches, and trunk. These decorticated areas tend to be small on twigs but are larger on branches and trunks. Indeed, near the base of large shrubs they often cover most of the circumference of the trunk and the living bark may be restricted to narrow stripes (or a single stripe) separated by areas of dead bleached xylem. I call this condition "bark striping". In older individuals, unequal radial growth resulting from the unequal circumferential distribution of active vascular cambium (bark stripes) results in the development of markedly gnarled and flattened stems. Where stems are slanted or horizontal the bark stripe is often found on the underside of the stem. It is the purpose of this paper to suggest possible causes and a possible adaptive significance of bark striping.

Bark striping in manzanitas (*Arctostaphylos*) was first described in individuals of *A. myrtifolia* Parry and *A. viscida* Parry (Adams, 1934). Adams contended that the decorticated areas originate as small pathogen-induced "pustulous excrescences" located external to tangential separations between the current year's growth ring and the older xylem. The excrescence is occupied by a mass of "large, thick- and porous-walled cells", the inner surface of which is lined with cork tissue. He believed that these excrescences eventually rupture, forming lesions in the bark. Decortications resulting from these lesions are said to increase in size as a result of the vertical and circumferential progression of the margins of these lesions. Adams considered that the time involved in this progression explains the observation that decorticated areas are most pronounced on older stems. Gankin and Major (1964) also described bark striping for *A. myrtifolia*, but made no attempt to explain its origin.

Bark stripes have also been recorded on *Pinus aristata* Engelm. (Wright and Mooney, 1965; LaMarche, 1969) and many species of desert and Mediterranean shrubs (Waisel et al., 1972). Waisel et al. found that these shrubs are characterized by a sectorial pattern of water ascent and that from a functional point of view, "such plants are composed of a group of independent smaller units, each composed of a branch and a root which are connected by a continuous vascular system". Death of certain superficial units could result in the development of decortications and bark stripes.

I have found that bark striping is common in *Arctostaphylos andersonii* Gray, *A. auriculata* Eastw., *A. glutinosa* Schreib., *A. hooveri* P. V.

Wells, *A. insularis* Greene, *A. montarensis* Roof, *A. pajaroensis* Adams, *A. pallida* Eastw., and *A. regismontana* Eastw. Three observations concerning these stripes seem pertinent to a discussion of their origin: (1) Adams never actually found pathogens associated with developing decortications; (2) small dead areas on the younger branches are often covered with desiccated bark that shows no evidence of the rupturing that Adams described; and (3) the apical ends of most decorticated areas are associated distally with dead portions of the shrub such as shaded branch systems, burned branch systems, broken branches, and clusters of dead leaves. These observations lead me to suggest that the development of decorticated areas on the stems of manzanitas is initiated by non-pathological environmental influences such as shade, fire, soil moisture stress, and extremes of temperature.

Manzanitas are intolerant of shade (Davis, 1972). Shaded leaves soon wither and die whether the source of shade is the higher branches of the same shrub or those of a neighboring plant. The twigs and branches supporting these leaves then become desiccated and also die. A progressive death of twigs and branches, due to the loss of functional leaves, continues basally until a branch is reached that contains vascular traces that are still associated with functional leaves. Such a branch usually shows some degree of bark striping. The extent of bark striping is inversely related to the extent of shading. The greater the percentage of shade-killed leaves and twigs in a branch system, the smaller is the proportion of living bark on the supporting branch.

The effects of fire may be similar to those of shading. If a fire kills only a portion of a shrub, the resulting decorticated area will be associated with those branch systems that are burned. This relationship can be seen in individuals of *A. glutinosa* growing on outcrops of Monterey shale in Santa Cruz County. A fire in 1950 destroyed many of these non-sprouting manzanitas, but some were damaged only on one side. In these instances, decortications are found on the side of the shrub that faced the fire. Some of these decortications appear to have been caused by burning of the vascular cambium. However, other decortications are not burned or scorched and must have been caused by the death of the upper branches and leaves that were burned.

Root desiccation may be another cause of bark striping. Certain individuals of *A. auriculata* growing on xeric sites in open sun and showing no signs of fire damage have conspicuous decorticated areas leading up to dead branch systems. Waisel et al. (1972) noted that "in cases where one single root was desiccated, only that branch which was connected to the root was damaged and the vitality of the entire crown remained unaffected". It seems probable that the desiccation of certain roots on these xeric sites could result in the formation of decortications and the death of branch systems and leaf clusters at the terminus of the decorticated areas.

In the preceding examples the development of decorticated areas appears to be a secondary response to leaf or root mortality. However, the development of living bark stripes on the underside of slanted and horizontal stems may be a direct result of sun damage. Young, horizontal branches, especially those occurring near the ground, often retain patches of dead, desiccated bark on their upper surfaces. Cross-sections of these branches frequently reveal that their growth rings are thicker on the lower side. It seems possible that these types of morphological alterations could result from sun-induced death of the phellogen and suppression of cell division in the vascular cambium on the upper side of these branches.

An alternate explanation for the development of bark stripes on the underside of horizontal branches evolves from the fact that twigs arising from the underside of a branch are usually short-lived because their leaves are soon killed by shading. These small twigs are easily buried by the developing secondary xylem of the supporting branch. However, twigs on the upper side of a branch may survive for several years before succumbing to the effects of shade from the ever-widening canopy of the shrub (Davis, 1972). Their ultimate death could add an extensive volume of non-functional vascular tissue to the upper surface of the horizontal supporting branch. This could result in the development of decortications that would restrict functional vascular tissues to a lateral or inferior position on the branch.

The mechanism by which leaf cluster or root death can result in the development of decortications on the intervening branches may involve the death of the vascular cambium in the branch of desiccation. In fully corticated branches the heartwood is completely surrounded by functional xylem associated with functional leaves. As long as these branch systems develop symmetrically, no major decortications are likely to occur. However, when environmental influences, such as unilateral shading, kill certain branch systems, non-functional traces from these branch systems will accumulate on the side of the supporting branch experiencing the death of leaves and twigs. Decortications develop where these non-functional vascular traces lie so close to the surface of the branch that they effectively interrupt the movement of water from functional xylem elements to the overlying cambium. Such decortications often originate at the point of insertion of a dead twig or branch because in these areas the non-functional traces lie immediately beneath the cambium of the branch. Farther down the branch, traces from living leaves usually lie between the dead traces and the cambium. However, island decortications might arise where this layer of functional xylem is discontinuous. Enlargement and coalescence of decortications result from the addition of traces from higher leaves as these leaves die. Essentially the same process would occur in the cases where root death initiates the formation of decortications.

Some decortications arise at scattered locations on the surface of twigs and young branches, are not associated with superficial non-functional traces, and do not appear to be directly related to the death of leaf clusters or roots. It is possible that these decortications develop in response to damage caused to the cambium and other superficial tissues by the formation of ring shakes in the outer layer of the xylem. A ring shake is tangential separation of the xylem between or within growth rings. Koehler (1933) noted that shakes "are due to transverse compression and tension stresses . . ." and cited chemically-induced shrinkage of the older wood, reduction in turgidity of the older wood in the trunk, and greater circumferential than radial growth as potential sources for such stresses. Brown et al. (1949) also cited the shrinkage of the heartwood as a source of ring shakes. I suggest that the tangential separations observed by Adams (1934) are ring shakes that form in response to shrinkage of non-functional vascular traces deeper in the stem, excessive circumferential growth (as on the surface of rapidly enlarging bark stripes), or a combination of the two, and that his cork tissue and "large, thick- and porous-walled cells" are a form of wound tissue that develops in response to the formation of the shakes. Ring shakes tend to form along lines of weakness (such as annual rings) and may increase in size along these lines. Decortications may arise where ring shakes and their associated wound tissue attain sufficient size to interfere with the radial movement of water to the cambium and other superficial tissues.

Whatever their mode of origin, bark stripes certainly represent a positive adaptation to the Mediterranean climate and chaparral vegetation of the central coast ranges of California. Shrubs and trees living in this region must be able to withstand fire, seasonal drought, and shading. Fire usually destroys non-sprouting manzanitas and, where fires are frequent, these shrubs fail to attain maximum size. However, in areas protected from fire or where fires are infrequent, they often become very large (4 to 7 m tall) and may eventually assume dominance on the site. In order to accomplish this, these shade-intolerant manzanitas must accrue sufficient height each year to maintain their canopies in open sunlight. The continued increase in height in a region where extended summer drought restricts shrub size is facilitated by the processes leading to the formation of bark stripes. Water loss through transpiration is reduced by the loss of all but the most healthy, vigorous, and well illuminated leaves, and excessive non-photosynthetic tissue is eliminated by the inactivation and death of axial vascular tissues associated with dead leaves or roots. Growth continues at viable meristems but the volume of living shrub may increase little or not at all since any increment of new tissues added by the meristems is apt to be cancelled by the inactivation and death of older tissues. As the shrub ages, the proportion of functional wood decreases and decortications begin to

form. In large shrubs the percentage of the shoot composed of living stripes is often small compared to that composed of dead wood. The net result of this growth pattern is a "vine-like" manzanita shrub supported and held aloft by its own dead remains.

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LITERATURE OF INTEREST

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Annual review of ecology and systematics. R. F. Johnston, Ed. Vol. 3, 1972. Annual Reviews Inc., Palo Alto. Sixteen review papers on diverse topics, including mineral cycling, niche theory, community interactions on marine rocky intertidal shores, the carbon balance of plants, cladistic methodology, and geographic variation.

The North American species of *Psathyrella*. Alexander H. Smith. 1972. *Memoirs New York Bot. Gard.* 24:1-633. \$35.00. An illustrated monographic treatment of 414 species of the agarical genus *Psathyrella*.

The polygamous species of the genus *Galium* (Rubiaceae) section *Lophogalum*, of Mexico and southwestern United States. Lauramay T. Dempster. 1973. *Univ. Calif. Publ. Bot.* 64:1-36. \$2.50. An illustrated monograph of 14 species of *Galium*, four of which are newly described.

ADDITIONAL PLANT RECORDS FOR OREGON.—We wish to report some new species records, based on specimens in the Oregon State University Herbarium (OSC), and to comment on the distribution of some adventive species that have been ascribed to the state by C. L. Hitchcock et al. (*Vascular plants of the Pacific Northwest*, Parts 1-5, 1955-1969). Of the plants listed, only one (*Antirrhinum*) is mentioned in M. E. Peck's *Manual of the higher plants of Oregon* (Ed. 2, 1961).

Panicum dichotomiflorum Michx. was reported in our area only from Adams County, Idaho (Hitchcock, Part 1, 1969), but we have specimens from Ontario, Malheur County (*L. Bailey*, in 1963) and Talent, Jackson County (*Reimer*, in 1940).

Polygonum scabrum Moench is cited from Oregon by Fernald (*Gray's Manual of Botany*, 8th Ed., 1950) but has been omitted from all the manuals and floras of the state. It occurs in gravel pits on the river floodplains in Benton County (*L. J. Dennis* 2774, near the Long Tom River).

Cerastium siculum Guss. was received by us from La Grande, Union County, in 1969 (*E. J. Kirsch*). It readily fits the description by Hitchcock (Part 2, 1964), who notes the occurrence of this species near Pullman, Washington, since before 1944.

Gypsophila paniculata L. also is part of the adventive flora of Oregon. At OSC are a 1956 collection from Klamath Falls (*H. Schieferstein*) and one in 1969 from a vacant lot in Burns, Harney County (*R. B. Roberts*). It is not known how well established these populations are.

Clematis vitalba L. is adventive in Portland, Multnomah County (*Mrs. Evelyn Hall*, in 1956 and 1957). Hitchcock (Part 2, 1964) states it is established in the Puget Sound region.

Trollius laxus Salisb. enters the northeast corner of Oregon in Wallowa County, according to a collection by Helen M. Gilkey (in 1940) from a "spring near Hat Point".

Sedum purdyi Jeps., a species of northern California, has been found in southern Jackson County, in the Squaw Lakes region of the upper Applegate River (*Mrs. L. C. Grothaus*, in 1964).

Onobrychis viciaefolia Scop. is reported as naturalized at the headquarters of the Squaw Butte Range Experimental Area, Harney County (*Steward & Smith*, in 1958, identified by Terry E. Northstrom).

Trifolium vesiculosum Savi, collected and identified by Dr. Duane Isely (11302, in 1971), occurs in waste areas along Highway 99W in South Corvallis, Benton County.

Geranium lucidum L. has been collected at two localities in Yamhill County: *L. H. Gross* (in 1972), northwest of Yamhill; and *Judy Jernstedt* 46 (in 1972), southeast of Carlton. It is said to be fairly common, both in wet pastures and in coniferous woods.

Geranium robertianum L. is established in at least two sites in Benton County west of Corvallis. It is abundant at an archery range near Wren, and was collected at Kings Valley in 1958 by Helen M. Gilkey. Hitchcock (Part 1, 1969) cites it from Portland and parts of western Washington.

Euphorbia esula L. was not credited to Oregon by Hitchcock (Part 3, 1961), probably by oversight since it is mentioned by Helen Gilkey in *Weeds of the Pacific Northwest* (1957). There are specimens at OSC from the following counties: Benton, Grant, Jackson, Klamath, and Wallowa.

Peganum harmala L. was found near Prineville, Crook County (*E. Wood*, in 1967). Hitchcock (Part 3, 1961) reported its occurrence at Ephrata, Washington.

Hibiscus trionum L., mentioned by Hitchcock (Part 1, 1969) as adventive in the Willamette Valley, grows also near Roseburg in Douglas County (*J. R. Parker*, in 1957) and near Medford in Jackson County (*D. Gentner*, in 1947).

Antirrhinum orontium L. is more widely and commonly established in Oregon than references by Cronquist in Hitchcock et al. (Part 4, 1959; Part 1, 1969) would indicate. We have specimens from the following counties: Benton, Columbia, Lincoln, Linn, Multnomah, and Wasco.

Gnaphalium collinum Labill. is a weedy adventive in coastal Curry County, between Brookings and Gold Beach (*L. J. Dennis* 2694; *K. L. Chambers* 2241). Munz (*A California Flora*, 1959) reported it from Humboldt and Del Norte counties.

Haplopappus arborescens (Gray) Hall has been verified for Oregon by two recent collections from Curry County (Mt. Emily, *A. Mikkelsen*, in 1971; Snake-tooth Butte, *W. Schroeder*, in 1972).—KENTON L. CHAMBERS and LAREA J. DENNIS, Oregon State University, Corvallis 97331.

A NEW CALIFORNIA RECORD FOR *FILAGO VULGARIS*.—On May 28 and on July 3, 1971, Elizabeth Lennon collected *Filago vulgaris* Lamarck in Marin County, California, where it grew on open slopes above Kirby Cove just west of the Golden Gate Bridge. This is the third record of this Old World plant to be reported from the Pacific States, the other two being from Douglas County, Oregon (Leaf. W. Bot. 2:192. 1939), and from Mendocino County, California (Leaf. W. Bot. 3:168. 1942). In those two notes, I reported the plant as *Gifola germanica* (L.) Dumort., but here I am following Wagenitz (Willdenowia 4:51. 1965), who has shown that Lamarck's name is the one to be used.

This distinctive cudweed is all but omitted from our western floras: the Mendocino County occurrence has now been noted by Munz (Supplement to a California flora, 1968, p. 164), but it was omitted in both editions of Peck's *Manual of the higher plants of Oregon* (1941; 1961), and in both printings of Munz' *A California flora* (1959; 1963). Since the plant has now a known linear distribution of nearly 500 miles in California and Oregon, one wonders whether it is truly a rare weed or whether it is more common and has been overlooked by collectors because of its superficial resemblance to some of our more ubiquitous cudweeds.—JOHN THOMAS HOWELL, California Academy of Sciences, San Francisco 94118.

NOTES ON WESTERN MYXOMYCETES.—

1. The demise of *Didymium aurantipes* Brooks & Kowalski.—In the summer of 1971, while studying the myxomycete collections at the Royal Botanic Gardens, Kew, I examined a specimen labeled *Didymium laxifila* G. Lister & Ross (Essex Nat. 27:263–264. 1945) collected by Ross from the type locality (*Ross 3501*, on dead leaves, Loughton, Epping Forest, Sussex, England, Jan. 19, 1944). Presumably, this represents the type collection. Comparing this specimen with the type and numerous other collections of *Didymium aurantipes* Brooks & Kowalski (Mycologia 58:169–173. 1966) that I have made in California indicates that the two species are identical in all particulars. Thus, *D. aurantipes* is a synonym of *D. laxifila*.

2. Concerning *Physarum albescens* Ellis ex Macbr. and *Physarum rubronodum* Martin.—*Physarum albescens* is a very common snowline myxomycete found abundantly throughout the alpine areas of the western states. While I have collected *P. albescens* on numerous occasions, I never found material that seemed to fit *Physarum rubronodum*. I was especially curious why this was so, since *P. rubronodum* was described from the slopes of Mt. Shasta (Jour. Wash. Acad. 38:238–240. 1948) and I have spent many hours collecting in that area. Recently I obtained the type collection of *P. rubronodum* (IA) and the reason for my not collecting it became clear. It is the same as *P. albescens*.

Physarum albescens is a remarkably variable taxon and in my opinion the descriptions given it in the numerous monographs of myxomycetes do not indicate its extreme variability. Thus, a detailed description follows:

PHYSARUM ALBESCENS Ellis ex Macbr., N. Am. Slime-Moulds ed. 2. 86. 1922.

Leocarpus fulvus Macbr., N. Am. Slime-Moulds 82. 1899.

Physarum fulvum (Macbr.) G. Lister, Mycet. ed. 2. 60. 1911. Not *P. fulvum* Fries, 1829.

Physarum rubronodum Martin, Jour. Wash. Acad. 38:238. 1948.

Sporangia loosely to densely gregarious, rarely scattered, subglobose to shortly plasmodiocarpous or, more commonly, obovoid, sessile, or, more commonly, borne on strand-like extensions of the hypothallus, 0.7–1.5 mm in diameter, up to 2.0 mm in height, white, pale to brilliant yellow, light to dark orange or, when lime is lacking, dark blue, dehiscing above in small flakes, tending to be persistent below; peridium basically single, when the limy crust is especially thick, appearing double as the lime flakes off, membranous and iridescent when lime is lacking, thick and crustose when charged with lime; stipe, when present, simply an extension of the hypothallus, up to 2.0 mm in length; hypothallus massive, venulose, composed of

flattened, thick, overlapping strands, creamy yellow to light orange; columella absent; capillitium dark brown to more commonly, pallid, forming a very rigid, intricate reticulum with numerous free ends, occasionally somewhat elastic, attached to the peridium, threads flattened, rarely expanded in the axils, lime knots highly variable, sparse to numerous, minute to large, round, elongated or branched, yellow, orange, red, or white, rarely aggregated in the center of the sporangium to form an irregular, small to massive pseudocolumella; spores globose, black to dark purple-brown in mass, purple to violet-brown by transmitted light, 11–13 μ in diameter, spinulose, often lighter on one side; plasmodium yellow (Martin and Alexopoulos, *The Myxomycetes*. Univ. Iowa Press. 1969) to scarlet or orange-red.

The following collections, upon which the above description was based, have been deposited in UC: Kowalski 2973, 2977, 2978, 2981, 2988, 3076, 3106, 3411, 6078, 6335, 6605, 6865, 7476, 11027, 11041, 11664.

3. A new name for *Comatricha suksdorfii* var. *aggregata* Meylan.—When I first began collecting western slime molds in 1964 I frequently encountered an alpine species that keyed out to *Comatricha suksdorfii* Ellis & Ev. in Martin's 1949 monograph (*North Am. Flora* 1(1):1–190). In their 1969 book Martin and Alexopoulos (*ibid.*) placed *Comatricha pacifica* Macbr. in synonymy with *C. suksdorfii*. I recently examined the type collections of both taxa and agree with their placement. The species I had been calling *C. suksdorfii*, however, is neither of these taxa, nor does it fit any species of *Comatricha* in their 1969 work. A detailed search of the literature and the subsequent observation of a Meylan collection, which is presumably the type, indicates it is the same as *C. suksdorfii* var. *aggregata* Meylan (*Bull. Soc. Vaud. Sci. Nat.* 53:451–463. 1921). I have made over 100 collections of Meylan's variety and *C. suksdorfii* var. *suksdorfii* and it is my opinion that the two varieties are sufficiently distinct to justify their placement in separate species. The name *C. aggregata* cannot be used since it was used for a different species by Farr (*Bull. Inst. Jamaica, Sci. ser.* 7:1–67. 1957). I am proposing a new name and giving a detailed description since Meylan's description was very short and incomplete and because this species is extremely common in montane regions and has probably been collected by numerous workers in the past.

***Comatricha alpina* Kowalski, nom. et stat. nov.**

Comatricha suksdorfii var. *aggregata* Meylan, *Bull. Soc. Vaud. Sci. Nat.* 53:455. 1921.

Sporangia densely caespitose, jet black when the spores are present, purple-brown when the spores are blown out, cylindrical, but tapering slightly at the apex, 1.5–3.0 mm in height, 0.5–1.0 mm in width; stipes short, 1.0 mm or less in length, black, setaceous; peridium entirely fugacious; hypothallus continuous, dark brown to black at the base of the stipe, becoming orangish towards the periphery; columella a continuation of the stipe, black, cylindrical, but tapering slightly and becoming irregular at the apex, ending just below the apex of the sporangium, giving rise to the capillitium evenly along its entire length; capillitium rigid, composed of branching and anastomosing threads that form a dense reticulum with numerous free ends; spores globose, black in mass, purple-brown by transmitted light, 11–12 μ in diameter, minutely but densely spinulose, lighter on one side; plasmodium unknown.

The following collections of this taxon have also been deposited in UC: Kowalski 1901, 2994, 3014, 3123, 3401, 3621, 6691, 6706, 6958.

There is no question that *C. alpina* and *C. suksdorfii* are closely related. They are both snowline myxomycetes found only at high elevations near melting snow in late spring or early summer. They are also cylindrical in shape, jet black in mass, produce rigid, dense, net-like capillitia, and have spores that are essentially identical. Their differences, however, can easily be discerned by the naked eye. These are as follows: in *C. suksdorfii* the sporangia are widely scattered, there often being 2.0 mm or more between individual sporangia, the peridium often remains as small frag-

ments, and due to the long stipes, approaching 4.0 mm in length, the overall size is very large, occasionally attaining 8.0 mm. In *C. alpina* the sporangia are densely clustered so that the individual sperangia are always in contact with one another, the peridium is entirely evanescent, and due to the short stipes, 1.0 mm or less in length, the overall size is much smaller, rarely attaining a maximum of 4.0 mm.

I wish to express my appreciation to the following individuals for the loan of material used during the course of this investigation: H. Cléménçon, Curator for Cryptogams, Université de Lausanne, Institut de Botanique Systématique et de Géobotanique, Lausanne, Switzerland; R. L. Hulbary, Chairman, Department of Botany, University of Iowa, Iowa City. This work was supported by the National Science Foundation grant GB-2865.—DONALD T. KOWALSKI, Department of Biological Sciences, California State University, Chico 95926.

CALIFORNIA VEGETATION-TYPE MAPS AVAILABLE.—Limited quantities of 21 vegetation-type maps of topographic quadrangles in California have recently become available for free distribution. The maps show the dominant vegetation of parts of California as it existed about four decades ago. Colors and symbols denoting the vegetation types are overprinted on U. S. Geological Survey maps. Published in 1932-1940, the maps are the product of field work done in 1927-1934 by the Vegetation-Type Map survey of the U.S. Forest Service. The vegetation types and field mapping procedures used in this survey have been described briefly in recent publication (Critchfield, William B. 1971. Profiles of California vegetation. USDA Forest Service Research Paper PSW-76. Pacific SW. Forest & Range Exp. Sta., Berkeley, Calif.) Requests for copies of the maps, including map number and name, should be addressed to the Pacific Southwest Forest and Range Experiment Station, P. O. Box 245, Berkeley, California 94701.

List of Vegetation-Type Maps

Number	Name	Location (NE corner)	
		Latitude	Longitude
30-minute quadrangles:			
23	Redding	41°00'	122°00'
153	Elizabeth Lake	35°00'	118°00'
165	San Gorgonio	34°30'	116°30'
175	San Jacinto	34°00'	116°30'
176	Elsinore	34°00'	117°00'
177	Corona	34°00'	117°30'
181	Ramona	33°30'	116°30'
15-minute quadrangles:			
82C	San Mateo	37°45'	122°15'
161A	Santa Susana	34°30'	118°30'
161B	Piru	34°30'	118°45'
161C	Triunfo Pass	34°15'	118°45'
161D	Calabasas	34°15'	118°30'
162A	Tujunga	34°30'	118°00'
162B	San Fernando	34°30'	118°15'
162D	Pasadena	34°15'	118°00'
163A	San Antonio	34°30'	117°30'
163B	Rock Creek	34°30'	117°45'
163C	Pomona	34°15'	117°45'
163D	Cucamonga	34°15'	117°30'
164C	San Bernardino	34°15'	117°15'
164D	Redlands	34°15'	117°00'

NOTES AND NEWS

VALIDATION OF TRANSFER OF *ECTOCARPUS MUCRONATUS* TO *GIFFORDIA*.—The transfer of *Ectocarpus mucronatus* Saunders (Proc. Calif. Acad. Sci., ser. 3, Bot. 1:152, pl. xix. 1898) on p. 90 of Madroño, vol. 22, 1973, is invalid because the place and date of publication of the basionym were omitted. The new combination, *Giffordia mucronata* (Saunders) Kjeldsen and Phinney, is made valid here.—CHRIS K. KJELDSEN, Biology Department, California State College—Sonoma, Rohnert Park 94928, and HARRY K. PHINNEY, Botany Department, Oregon State University, Corvallis 97331.

REVIEWS

Alpine rangelands of the Uinta Mountains and Flora and major plant communities of the Ruby-East Humboldt Mountains. By Mont E. Lewis. 75 & 62 pp. U. S. Forest Service, Region 4, Ogden, Utah. 1970 & 1971.

The U. S. Forest Service is an honest, conscientious, large, wide-flung, old, and generally expert government bureau that manages the bases of production for much of the West's lumber and livestock industries, the water that is vital to everyone in the West, and the open-space amenities that are indispensable. It is currently being criticized. Local residents object to clear-cutting forests in a travesty of sustained yield, and lumbermen want a larger annual cut from federal lands to brake the price rise on lumber so privately-owned timber will have a future market. Conservationists object to management that destroys resources; commercial interests object to preservation of wilderness areas. Foresters want to convert old-growth stands to "healthy, rapidly growing, managed forests"; others believe the necessary silvicultural knowledge is too poor, call the process mining and the result brush fields. Some emphasize the relief from urban existence experienced in the woods; others say Americans cannot be housed without making 2×4 's out of the remnants of our virgin forests. Resort developers want to build private country clubs on public land; hikers have always hiked for free. Most western ski resorts have been developed on Forest Service lands and according to Forest Service plans; many skiers object to the very expensive yo-yoing on the pattycaked piste that skiing has become. Organized skiing wants more lift-served areas; many skiers object that touring areas have been preempted for purely commercial purposes. So it is nice to be able to say nothing but good about the two recent Forest Service publications by M. E. Lewis.

The plant cover of none of the mountain ranges of the western U. S. is so well studied that another look by an expert is not very welcome. These two papers are administrative studies, inventories, descriptions made to assist the U. S. Forest Service in discharging its administrative responsibilities, but they also contain new basic information and update older ecological work.

They are the result of careful, long-continued, and perceptive observations by an experienced field botanist. They are basic to management of the Wasatch, Ashley, and Humboldt National Forests. They are basic to understanding the plant ecology of the Ruby Mts. of eastern Nevada and Uinta Mts. of northeastern Utah. They could have been done only by a skilled field taxonomist who is also a knowledgeable and sensitive ecologist.

They both contain checklists of the plant species, 577 for the Rubies and 357 for the Uintas. For the Uintas the species are listed by habitat types, for the Rubies by major plant communities (altitudinal belts) with notes on abundance and kinds of habitats. described physiognomically. Such local data contribute to autecology and therefore to inductive rather than anecdotal descriptions of plant habitats in floras. For once species of *Carex* are decently treated in floristic and vegetational analyses.

The Uintas are not only the highest mountain range in Utah but the largest

east-west trending one in the U. S., although the significance of this orientation in producing a unique climate has never been evaluated. They are also the site of a very large-scale natural experiment on vegetation, namely the recent natural migration and successful multiplication of moose (*Alces*) into a suitable habitat formerly without them.

A variety of plant communities was recognized by Lewis in the Uintas. Lists of species are given for each. Unfortunately the basic stand surveys are not tabulated, so conclusions only, not data, are presented. This is, sad to say, a universal practice in American plant ecology. It distinguishes our work from that in the rest of the world. There the Braun-Blanquet system of presenting tables of species occurrences on individual sites (stands) is almost universal, and it makes possible agreement or disagreement on the hypothesis that certain species do in fact occur together in ecologically homogeneous areas often enough to make the recognition of such associations valuable not only to describe vegetation but to indicate its ecology.

The Uinta booklet is an excellent review of alpine plant ecology, well-summarized and well-illustrated. It integrates the effects of topography, soils, frost action on soils, snow cover, and sheep grazing on the species composition, abundance, and dry weight production of the plant cover. The photograph on page 12 shows a fascinating combination of bare and vegetated surfaces that, according to the reviewer's bias, will never be explained until someone sees it during most of the year—when the snow first comes, when it melts, when the ground freezes, deeply or as needle ice, when ground thaws, when and where rodents are active, what grazing sheep, or other herbivores, do, etc.

Lewis presents a framework of hypothetical successional relationships, "Climax is herein used with reservation. The described communities, rather than replacing one another, may be a reflection of the specific environment" (p. 45).

The Rubies occupy a unique place in western American phytogeography as was apparent from A. H. Holmgren's *Handbook of the vascular plants of northeastern Nevada* (1942, Utah State Agric. College, Logan and U. S. Grazing Service, Elko) and emphasized in L. L. Loope's recent floristically oriented work (1969, *Subalpine and alpine vegetation of northeastern Nevada*, PhD thesis, Duke University, Durham, North Carolina). Graphic evidence is on the maps in Hultén's *Flora of Alaska and neighboring territories* (1968, Stanford U. Press) where numerous northern species have an isolated station far out in the Great Basin from the Rocky Mountain ranges, namely in the Rubies.

In the Ruby Mountains study one of Lewis' main objectives was "to make at least a tentative classification of the plant communities" (p. 4). Stand surveys were made but are not always listed separately. The vegetation is described simply, mostly by dominance. The scheme used is one the man on the ground sees, not a theoretical one. Theory follows. The scaled values of abundance recorded have no advantage over older ones (Hult-Sernander, Braun-Blanquet, Domin) but the disadvantage of having been used in only one other study. In Lewis' paper are compositional data on and discussions of pinyon-juniper, sagebrush, *Cercocarpus ledifolius*, *Ceanothus velutinus*, *Populus tremuloides*, subalpine conifer, shrub, tall forb and meadow and alpine vegetation. Bibliographies for each type are given.

Both these papers are progress reports. They record much progress.

Is there any way students who study the ecology of some kind of vegetation or the vegetation of some area can be brought up to the field taxonomic competence that Lewis has? Or must they (we) all become measurers of temperature, of radiation, of rain, of soil particle sizes, of photosynthesis, of transpiration, of above- and below ground biomass, etc.? Not that these measurements are not worth doing. They certainly are. But someone, sometime, has to describe what plants occur together in the fascinating natural mosaic that can tell us so much about the history and ecology of our flora and vegetation.—JACK MAJOR, Botany Department, University of California, Davis 95616.

Intermountain Flora: Vascular Plants of the Intermountain West, U. S. A. Volume I. By ARTHUR CRONQUIST, ARTHUR H. HOLMGREN, NOEL H. HOLMGREN and JAMES L. REVEAL. Frontispiece, 270 pp., 102 numbered figures, 81 line drawings. Hafner Publishing Co., Inc., New York and London. 1972. \$17.50.

This is the first volume of a projected six-volume work designed to provide the first illustrated flora of a vast dry-land region covering the Great Basin Floristic Province including all of Utah, most of Nevada, large parts of Oregon and Idaho and smaller sections of Wyoming, Arizona, and California. And although this is not part of their claim, the books will provide an effective illustrated flora of the western half of Colorado as well, a bonus for which West-slope educators and amateurs will be most grateful.

The designers of the Intermountain Flora project have had over thirty years to mature its format and to mark and guard against the mistakes and errors of omission and commission of all of its sibs. That they chose to adopt the multi-volume bookshelf, 8 x 10 $\frac{3}{4}$ ", slick-paper format may disappoint those who were hoping for a portable field-guide, but one has to admit that the product is magnificent. This more affluent production invites comparison with the recent *Vascular Plants of the Pacific Northwest*. In *Intermountain Flora*, a return to letterpress makes possible the compression into 89 pages of the same amount of material that occupies 133 pages in the other. The binding problem, which was literally the "undoing" of VPPNW, seems to have been corrected with a sturdy product in a pleasing russet "canyonlands" color. The choice of the recently-segregated *Pinus longaeva* for the cover and frontispiece may reflect the hopes of the authors for a book that will stand the test of time in many ways.

An introductory chapter gives the background and rationale of the work, with portraits of the authors. This is followed by four chapters on Physiography, Evolution of Floras (mostly fossil), Botanical Exploration, and Plant Geography (Floristic divisions, and Vegetation Zones). The first two chapters were contributed by W. D. Tidwell, S. R. Rushforth and D. Simper. The remaining chapters, as well as the short taxonomic section, covering the vascular cryptogams and gymnosperms, are unsigned. In most cases, the editorial "we" or "our" has been used, but the text lapses on page 193 into the first person singular in the discussion of the classification of the ferns, leading one to wonder which of the authors is speaking.

The line drawings by Jeanne Janish and her colleagues leave nothing to be desired; from gross habit to fine detail they are impeccable. Only a few minor errors occur. The captions under *Woodsia scopulina* and *W. oregana* (p. 219) should be transposed, and the plate caption (p. 225) misspells *Picea engelmannii*. Rather than restrict the illustrations to full pages, the format allows for them to share space with the text, making it possible to place illustrations close to the text reference. The taxonomic treatment provides invaluable references under the genus providing access to the source of more detailed literature, a practice that has been of immense value in Kearney & Peebles' *Arizona Flora*.

The chapter on taxonomic concepts leaves a good deal to be desired in explaining the use of the categories "subspecies" and "variety". Since the chapter was evidently created, like the legendary camel, by a committee, this is understandable. It does not help to sweep legitimate controversy under the rug by calling the variety the "ordinary" infraspecific category and the subspecies the "intercalary unit" between the species and variety. It is just as legitimate to call the subspecies the "ordinary" unit inasmuch as the categories have been used interchangeably for the major subsets of the species, especially those having geographic parameters. At any rate, to invent an oversimplified pragmatic definition of these categories and to ignore the serious discussions in the literature does nothing to resolve a very real problem concerning the use of trinomials in botanical nomenclature.

Volume I, with the omission of the very short taxonomic treatment, can stand on its own feet as a self-contained essay on the Intermountain Flora. It is very unfortunate that the publishers have "chained" this introduction to the subsequent

volumes. A larger printing of Volume I might have reached countless readers in schools and in ancillary fields who might have been led to purchase the entire set. This would have been a distinct contribution to education of the lay public, who in many instances will have no desire or funds to purchase the whole flora, but to whom we have an obligation to make known our concerns.

The introductory essays still are unfortunately too traditional and static or neglect some of the topics pertinent to the present world ecological crisis that could be well illustrated by the Intermountain region. For example, I miss a chapter on calciphily, gypsophily, selenophily and their relation to floristics, coupled with some report on the extent and impact of geobotanical prospecting methods (which have been carried on in some depth here) on the interdisciplinary aspects of systematic botany.

Utah and Nevada have had a history of drastic and continued overgrazing, but there is no discussion of its impact on the flora although the classic area of the Kaibab Plateau is included within the limits of the treatment. Nor is there any discussion of the history of the adventive flora, nor of the original geographic provenance of its weeds. Here, it seems to me, would be a great opportunity to show how the occurrence of weed species depends not only on the accident of introduction, but upon the selective pressure exerted on adventives by the local environment. The American distribution of Eurasian weed species provides a very sensitive indicator of the similarity of our local climates to those of the areas in which these weeds are indigenous in the Old World.

The volume would have benefited greatly from a full-dress discussion of the phenomenon of narrow endemism in arid areas and regions where isolated mountain ranges, deep river gorges, and great saline lakes provide an unexcelled laboratory for the investigation of evolution through edapho-climatic selection. A chapter discussing the actual and potential impact of reclamation dams and their fluctuating shorelines, of the stripmining of coal from the mesas and subsequent pollutants released by the power plants, and the effects of radioactive and other mining wastes upon the environment and its vegetation would also have been highly desirable.

Despite these drawbacks, the Intermountain Flora is the most ambitious attempt of the century to wed the traditional "taxonomists' flora" with much more interesting background of its history and development. Bassett Maguire is to be congratulated for having conceived the great plan and for having inspired so many capable students to carry through the work to completion. The New York Botanical Garden should be proud of the cooperative venture that it has helped to support. Colorado wishes it might have had the opportunity.—WILLIAM A. WEBER, University of Colorado Museum, Boulder 80302.

Keys to the Families and Genera of Queensland Flowering Plants (Magnoliophyta). By H. T. CLIFFORD and GWEN LUDLOW. 211 pp., illus. University of Queensland Press, St. Lucia, Queensland. 1972. \$9.50. (Available from International Scholarly Book Services Inc., P.O. Box 4347, Portland, OR 97208.)

The title of this small hard-bound volume quite fully describes its sparse contents. The keys to families and to genera seem to be adequate as regards the floral anatomy and general morphology of the taxa included. Because family descriptions based upon Queensland representatives are provided, the family keys offer rather minimal information. Somewhat more morphological information is included in the generic keys in as much as no generic descriptions, nor any other pertinent data, are offered. Thirty-five genera are illustrated by simple line drawings. The aim of

the book is to provide students a means of identifying Queensland plants to the correct family and genus. This stated aim is duly achieved. The volume should in this respect be useful to students and amateur naturalists in Queensland.

The disappointment of the reviewer, as an adopted Queenslander long fascinated with the flora of that much under-advertised Australian state, stems from the vast amount of available pertinent information excluded from the book. So much empty space is wasted in many of the family descriptions and almost all the keys, that one gets the impression that a minimum of information has been squeezed into a maximum of space. True, the authors did not intend the volume to serve as a flora of the state, but Professor Specht, in the foreword, does claim that the volume will serve as an interim handbook to the flora of Queensland. One perhaps could partially agree with him if at least a minimum of information about numbers of species per genera, whether indigenous or introduced, and some ecological and geographical information about each genus had been included. It seems evident that the authors, in their lack of interest in the ecological and geographic distribution of taxa, their indigenous vs. introduced status, and their phylogenetic relationships, are surely not floristic taxonomists, and could not have done much field work throughout Queensland.

In the hope that some of these shortcomings might be rectified in possible later editions of the "Keys", I should like to make respectfully a few suggestions. One suggestion that would require practically no space at all would be to indicate by an asterisk or some other symbol those families and genera that are not indigenous but are either naturalized or cultivated. The capriciousness with which cultivated taxa are included should be rectified to exclude all not naturalized or to include all commonly cultivated. Because perhaps one-third of the indigenous and two-thirds of the naturalized genera are represented by only one species in Queensland, a few words to indicate the habitat and area of the state in which each is found could easily be squeezed with the species name into the line now often represented by three words. For example, on the first page of keys to genera, the following changes might be made. Under the first family Casuarinaceae, the second genus *Gymnostoma* L. A. S. Johnson, that many of us recognize in Queensland, should at least be mentioned. The second and fourth families, Juglandaceae and Salicaceae, should be supplied with a symbol to indicate that they are introduced, not indigenous; or better, omitted altogether because none of their species are naturalized. For the third family Balanopsidaceae (Balanopaceae according to the International Code of Botanical Nomenclature) the line occupied by "Single genus . . . *Balanops*" could much more informatively read: "One species, montane rain forests, NE . . . *Balanops australiana*." Similarly for family number five, Fagaceae, "Single genus . . . *Nothofagus*", could be replaced by the line, "One species, temperate rain forests, Macpherson Range, SE . . . *Nothofagus moorei*." For family number six, Ulmaceae, "2 species, coastal forests" could easily be added to the line for *Celtis*, and "3 species, coastal forests" for *Trema*. "One species, rain forests, E. . . . *Aphananthe philippinensis*" probably would require an additional half-line for *Aphananthe*.

The classification used in "Keys" follows Melchior for dicots and Hutchinson for monocots, combining thereby some of the worst features of these two obsolescent classifications. Thus the highly specialized amentiferous, apetalous, and dioecious taxa are listed first, presumably as most primitive. Similarly, the last family treated is the Apostasiaceae, surely among the least specialized of all orchids. One could hope for a much more realistic, and more nearly phylogenetic, classification for a volume intended for students. The treatment of genera is relatively conservative, as is that for most of the dicot families. Some inconsistencies in the treatment of dicot families include the division of the Aizoaceae into Molluginaceae and Aizoaceae; whereas, the widely recognized Gyrostemonaceae is retained in the Phytolaccaceae. The cunoniaceous *Bauera* is retained in the Saxifragaceae and the Chrysobalanoideae in the Rosaceae, yet the three subfamilies of legumes are each raised to family rank. The Erythroxylaceae is not separated from the Linaceae nor *Sphenostemon* from

the Aquifoliaceae; yet, the Hippocrateaceae is segregated from the very closely related Celastraceae, *Leea* from the Vitaceae, *Sonneratia* from the Lythraceae, *Barringtonia* from the Lecythidaceae, Vacciniaceae from the Ericaceae, and *Brunonia* from the Goodeniaceae. The monocot families are very narrowly and unrealistically defined, following the Hutchinsonian tradition. I would treat the 223 families listed by Clifford and Ludlow as 201 valid families, including 175 indigenous, 6 naturalized, and 20 merely cultivated in Queensland.

Larger categories are greatly inflated. The class Angiospermae is, for example, elevated here to divisional status and called the Magnoliophyta. Similarly the monocot and dicot subclasses are elevated to class status as the Magnoliatae and Liliatae. This gross taxonomic inflation seems entirely unwarranted by the morphological facts. The Angiospermae appear to be no more distinct from each class of gymnosperms, like the Cordaitae, Cycadae, Ginkgoae, Coniferae, or Gnetae, than each of these is from one another in the quite adequate division Tracheophyta, the vascular plants.

I have noted few actual errors or serious omissions, either in fact or in typography. A few family names do not follow exactly the list of conserved family names in the International Code. A very few genera, mostly naturalized, have been omitted, and a few native genera appear to be placed in the wrong families. The volume is well-bound and attractively printed. On balance, this small book should find much use in Queensland even though I feel it falls far short of what it could have been with little extra effort or expenditure.—ROBERT F. THORNE, Rancho Santa Ana Botanic Garden, Claremont, California 91711.

Arctic Adaptations in Plants. By D. B. O. SAVILLE. 81 pp. Monograph no. 6, Research Branch, Canada Department of Agriculture. 1972. No price.

Douglas Saville is a member of the Plant Research Institute of the Canada Department of Agriculture, but he is the living answer to the mythical stereotype of a government scientist with tunnel vision. He has written learned papers on a very wide range of topics from the aerodynamics of the loon's wing to the taxonomy and evolution of the smut and rust fungi (with more than a pause among the flowering plants). Biogeography is one of his strong suits and his studies have carried him all over the Canadian Arctic and beyond. Consequently, he is the ideal author for this survey of arctic adaptations in plants—flowering plants, vascular cryptogams, bryophytes, lichens, algae, and his specially-beloved fungi.

Morphological, physiological, and reproductive aspects of adaptation are treated in relation to winter and summer survival through the vicissitudes of temperature, strong winds and snow abrasion, desiccation, low nitrogen supply, extremes of photoperiod, and the shortness of the growing season that afflict plants occupying arctic habitats. Simplicity of ecosystems and the low density of plant cover create their own special problems for solution. All of these matters are surveyed with an easy writing style and a degree of coverage that, if not exhaustive, is satisfying because it is a distillate from the comprehensive study of the subject by the author. This small book is essential reading for evolutionists and ecologists, even those who will never visit the arctic except vicariously through works such as this. It can be obtained from the Information Division, Canada Department of Agriculture, Ottawa, K1A 0C7.—HERBERT G. BAKER, Department of Botany, University of California, Berkeley 94720.

An Island Called California, An Ecological Introduction to Its Natural Communities. By ELNA S. BAKKER. xvi + 357 pp., illustrated with black and white photographs, line drawings, and maps. University of California Press, Berkeley. 1971. \$10.00, buckram.

The subtitle proclaims that this book is an ecological introduction to the natural communities of California. It may well be an introduction, but it is not a very good one.

The bulk of the text deals with a poorly delimited transect across California at about the latitude of San Francisco. Appended to this is a discussion of desert communities and occasional references to other parts of California. It is usually difficult to know what geographical area the author has in mind. For example, chaparral occurs virtually throughout the length of California, but it is hard to find a statement of its extent.

Scattered throughout are discussions of some of the factors that influence and determine plant and animal distributions. But almost any recent high school or college biology text states these principles better and more succinctly.

In my opinion, the author views nature in a rather uncritical and exclusively humanly orientated way. Evidence for this interpretation is the liberal use of such phrases as: "... loveliest of the sea weeds," (p. 6); "One uninvited dike dweller is a dreadful thing. Called furze, or gorse," (p. 47); "Mice are juicy feasts for keen-eyed and sharp-eared predators." (p. 57); "... streamside jungles of interior California valleys . . ." (p. 61); "So hungry are some individual trees of these species for light . . ." (p. 99); "The other members of this coniferous royal court are no mean princelings." (p. 185); "... sagebrush is firmly in command." (p. 226); "What strange little trees they are." (p. 248); "... boobum trees (*Idria colmnaris*)—giant hairy asparagus stalks . . ." (p. 297). With respect to this last entry, it should be pointed out that: a more appropriate common name is cirio; cirio does not occur in the United States as a native plant; and that the most recent work on the Fouquieriaceae places *Idria* within *Fouquieria*.

Perhaps because of a lack of knowledge or objectivity, a number of errors and misrepresentations have crept into the text. Some are listed here. On page 2 it is insinuated that no one was interested in ecology before the twentieth century. On page 17 the food pyramid would lead one to believe that hawks eat only snakes and rodents only seeds. Where does *Ulex europaeus* grow on salt marsh dikes (see p. 47)? The interpretation of the maintenance of grassland boundaries is simplistic (pp. 75–76). On page 85 the number of stands of *Cupressus abramsiana* is stated incorrectly. On pages 137, 152, and 157 vernal pools are mentioned, but the author completely ignores the interesting morphological and physiological adaptations of vernal pool plants and fails to mention the interesting patterns of endemism represented by them. Vernal pool is not in the index! On page 211 the author would have us believe that the corolla of *Cassiope* is attached to the calyx.

The author does, quite correctly accept the presence of fire as an environmental factor, but gives the impression that somehow she wishes it were not so.

Considerable space is taken up with discussions of situations outside of California. These seem to add little, even for comparative purposes.

In short, this book is a chatty, not very well organized account of some of the plants and animals in California with an attempt to explain why these occur where they do. I doubt that it will be very successful as a text. The fact that this reviewer's name is incorrectly cited in the bibliography does not increase his enthusiasm for this book.—JOHN H. THOMAS, Department of Biological Sciences, Stanford University, Stanford, California 94305.

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MIMULUS WIENSII (SCROPHULARIACEAE), A NEW SPECIES FROM WESTERN MEXICO

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On sunny, wet slopes in the pine forests of the Sierra Madre Occidental grow several populations of a wiry-stemmed, small, yellow-flowered *Mimulus*. They appear to be distinctly different (fig. 1) from any of the species of *Simiolus*, the section to which they apparently belong (Grant, 1924; Pennell, 1951). Therefore, on the basis of the reasons developed below, I propose recognizing them as a new species, named for Delbert Wiens, who was one of the first botanists to find them.

Mimulus wiensii Vickery, sp. nov. Ex affinitate *M. dentilobus* Rob. & Fern. et specierum affinium in toto distinguendus a caulibus filo metallico similibus, 5–24 cm in longitudine, folis subter persaepe purpureorubris, corollarum marginibus integris.

Annual herbs with loosely spreading branches; roots fibrous, slender; stems wiry, 5–24 cm long, slender, terete, glabrous to subglabrous, green to purplish-red, prostrate to ascending, rooting at the nodes; petioles glabrous to slightly hirsute, shorter than the leaves; leaves opposite, ovate to broadly ovate, 2–20 mm long, 3–13 mm wide, dentate, palmately 3–5 nerved, green above, green to purplish-red below, glabrous to occasionally sparsely white hairy towards the base; flowers axillary, pedicels glabrous, slender, longer than the blades; calyx obturbinate, 7–11 mm long, glabrous to sparsely hairy on the margins, green, more or less red-dotted, teeth triangular, upper one the longest, the two lower curving in; corolla 10–14 mm long, weakly bilabiate, yellow, tube red-dotted, lobes entire, style glabrous, less than one third as long as the calyx; stamens shorter than the tube; capsules oblong to ovate, half as long as the calyx, not beaked; seeds small, 0.5 mm long, yellow-brown, ovate to ellipsoidal, furrowed.

HABITAT: On wet, sunny slopes, in pine forests of the mountains.

DISTRIBUTION: Sierra Madre Occidental and Sierra de las Palmas, Mexico.

HOLOTYPE: West of El Salto, Durango, Mexico. Growing on wet banks near kilometer 1155 on the Durango-Mazatlan road. Elevation 2615 m. August 24, 1959, *Wiens 2643*, UT 76996.

METHODS AND MATERIALS

Three methods were used to investigate the relationships of *M. wiensii*. First, an experimental hybridization program was carried out. Plants of



FIG. 1. *Mimulus wiensii* Vickery. Drawing by Julian Maack.

greenhouse cultures of two populations of *M. wiensii*, one of *M. dentilobus* Rob. & Fern.—its most likely relative—and one of a local *M. glabratus* HBK. var. *glabratus*—the commonest *Mimulus* of the area—were intercrossed in all combinations (Table 1, fig. 2). Plants of each of these four cultures were intercrossed with plants of seven test populations representative of the other species of section *Simiolus* (Table 1, fig. 2). Seeds for these cultures were collected by the author or kindly supplied by A. Carter, H. S. Gentry, W. M. Hiesey, R. Holm, G. L. Stebbins, Jr., and D. Wiens. For each cross, nine flowers, on the average, were carefully hand-pollinated. The seeds produced were sown. The resulting F_1 hybrids were grown and self-pollinated by hand to ascertain their fertility. Second, the chromosome numbers of *M. wiensii*, the other key cultures, and of most of the test cultures were determined. The same cytological methods were employed as before (McArthur et al., 1972). Third, specimens of *M. wiensii* were compared morphologically with specimens of taxa to which they might belong or to which they might be closely related in the following herbaria: GH, MICH, TEX, UC, UT, BM, K, and W. Loans of specimens by K and MICH, the hospitality of the other herbaria, and support by the National Science Foundation (Grant No. 18139) are all much appreciated. Relevant herbarium specimens examined are as follows:

TABLE 1. ORIGINS OF THE MIMULUS CULTURES USED IN CROSSING EXPERIMENTS.

M. wiensii Vickery 6272: 100 m west of divide on Durango-Mazatlan Rd., Durango, Mexico, elev. 2,500 m, *Vickery* 2615 (10–15 cm form). 6273: 100 m west of divide on Durango-Mazatlan Rd., Durango, Mexico, elev. 2,500 m. *Vickery* 2616 (2–10 cm form).

M. dentilobus Rob. & Fern. 5324: Sierra Charro, Chihuahua, Mexico, *Gentry* 8073.

M. glabratus HBK. var. *glabratus* 6209: El Salto, km 1050 on Durango-Mazatlan Rd., Durango, Mexico, elev. 2,400 m, *Wiens* 2635.

M. glabratus var. *utahensis* Pennell 5048: Mono Lake, Mono County, California, elev. 1,935 m, *Stebbins* 714.

M. glabratus var. *fremontii* (Benth.) Grant 5063: Black Meadow, Whipple Mountains, San Bernardino County, California, April 21, 1940, UC 667,449 (collector unknown).

M. guttatus Fischer ex DC. (obligate annual forms) 5006: Yosemite Junction, Tuolumne County, California, elev. 390 m, *Hiesey* 560. 6181: Mt. Timpanogos, Wasatch County, Utah, elev. 2,500 m, *Vickery* 2370.

M. guttatus Fischer ex DC. (facultative perennial forms) 5052: Mt. Diablo, Contra Costa County, California, elev. 300 m, *Stebbins* 703. 5346: Mt. Oso, Stanislaus County, California, elev. 300 m, *Vickery* 190.

M. nasutus Greene (5754–3) 5865: Skagg's Springs, Sonoma County, California, elev. ca. 30 m, *Richard Holm*, spring 1951.

Mimulus wiensii Vickery. Holotype: *Wiens* 2634; near kilometer 1155 west of El Salto, Durango, Mexico; UT. Topotypes: *Vickery* 2615, 2616; UT. *McVaugh* 22835; near El Barroloso, Michoacan; MICH, US. *McVaugh* 12896; Nevado de Colima, above Canoa de Leoncito, Jalisco; US. *Ownbey & Ownbey* 1982; 34.9 km northeast of El Paraiso, Sinaloa; MICH, US. *Vickery* 2673; near El Palmito, Sinaloa; UT. *Vickery* 2675; near kilometer 1152, route 40, Durango; UT. *Wiens* 3521; 19 miles northwest of Santiago Papasquiaro, Durango; UT. (See also: *Gentry and Fox* 11,792 under *M. dentilobus*.)

Mimulus pennellii Gentry. Holotype: *Gentry* 5691; Africa, Sierra Ta-cuichamona, Sinaloa; MICH.

Mimulus dentilobus Robinson & Fernald. Holotype: *Hartman* 288; Nacori, Sonora; US *Carter* 2077; Arroyo Hondo, Cerro de la Giganta, Baja California del Sur; US, GH. *Gentry* 572 *M*; La Mesa Colorado, Sonora-Chihuahua; MICH. *Gentry* 7220; Penasco, Los Pucheros, Sierra Surotato, Sinaloa; MICH. *Gentry* 8073; Arroyo Hondo, Sierra Charuco, Chihuahua; MICH, UT. *Gentry* 8085; Rancho Byerly, Sierra Charuco, Chihuahua; MICH, US. *Gentry and Fox* 11,792; La Champagna, Sierra de las Palmas, south of Santa Rosalia, Baja California; MICH (sheet includes one specimen of *M. wiensii*). *Maguire*, May 23, 1935; Bear Canyon, 10 km east of Gila, Grand Co., New Mexico; UC, GH, US. *McVaugh* 7472; Horse Creek, Chinati Mountains, Presidio Co., Texas; MICH. *Pennell* 19,517; Arroyo Gochico, east of San Bernardo, Sonora; MICH, US.

Mimulus madrensis Seeman. Holotype: *Seeman* 2110, 1852–57; in swamps on the road from Durango to Tepic, Mexico; K, BM.

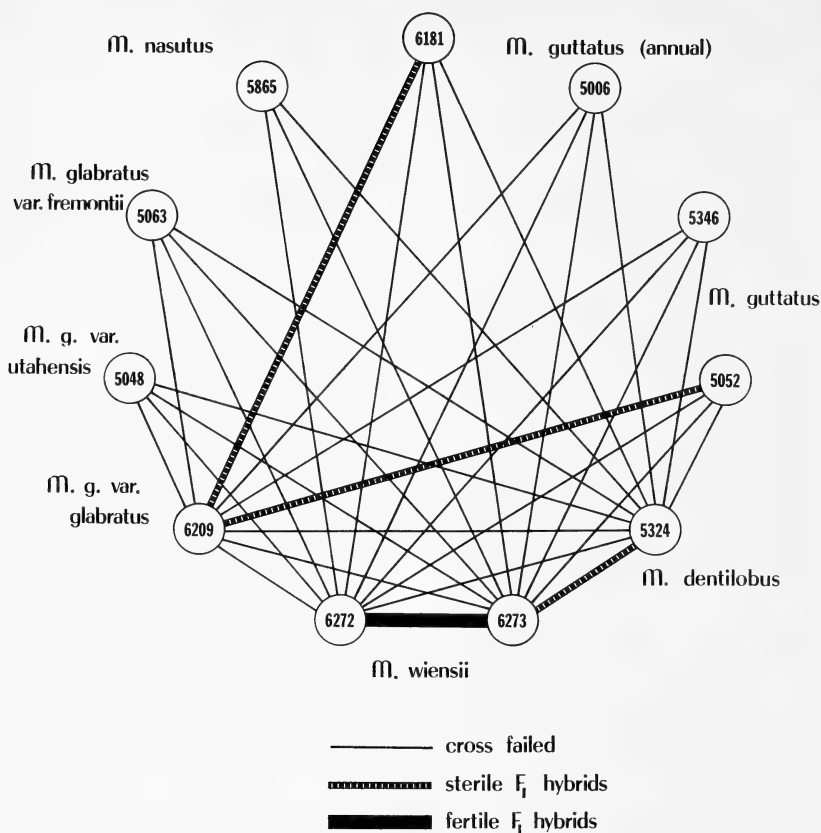


FIG. 2. Crossing relationships of cultures of *M. wiensii* Vickery and *M. dentilobus* Rob. & Fern. of the *Mimulus dentilobus* complex with each other and with representative taxa of the rest of section *Simiolus*.

Mimulus parvulus Wootton & Stanley. Holotype: Holzinger, Aug. 27-Sept. 12, 1911; Rocky Canyon, Mibres Valley, near Silver City, Grant Co., New Mexico; US.

RESULTS AND DISCUSSION

Experimental hybridization produced only five different F_1 hybrids from the 64 combinations tried (fig. 2). Two of the hybrids were the result of intercrossing the cultures of the two populations of *M. wiensii*, 6273×6272 and the reciprocal cross, 6272×6273 . Hybrids from the first cross had essentially normal fertility, 18 seeds per capsule compared to the parents' 5 and 42 seeds per capsule, respectively. The F_2 hybrids of this cross were vigorous and fertile also. However, 6272×6273 F_1 hybrids were sterile, that is, they set no seeds when self-pollinated. Intra-specific unidirectional barriers to gene exchange such as this, are well

known in *Mimulus* (Vickery, 1964, 1966, 1969). The third successful hybridization was between *M. dentilobus* and *M. wiensii*, 5324×6273 (fig. 2). This F_1 hybrid proved to be sterile too, but is remarkable in that it is the only combination in 76 different hybridizations attempted between *M. dentilobus* and other species of section *Simiolus* that produced a hybrid (Vickery, in press). Clearly, *M. dentilobus* is more closely related to *M. wiensii* than it is to any other species tested in section *Simiolus*. The last two successful hybridizations (fig. 2) did not involve either *M. wiensii* or *M. dentilobus*, but only the test cultures. Thus, *M. wiensii* exhibits a partial unidirectional barrier to gene exchange between its two populations tested, is completely isolated from its relative, *M. dentilobus*, by the sterility of the F_1 hybrids formed, and is separated from representative taxa of the rest of the section by a complete failure to produce viable hybrid seeds in the interpopulation crosses (fig. 2).

Cytological results are consistent with the crossing results. Both populations of *M. wiensii* and the one of *M. dentilobus* have $n = 16$ (Mukherjee et al., 1957; Mia et al., 1964). This is a unique chromosome number for section *Simiolus* except for distinctly different *M. gemmiparus* Weber, a propagule-producing species of the Rocky Mountains (Vickery et al., 1968; Weber, 1972). Of the test populations, the *M. guttatus* cultures 5006 and 5052 have $n = 14$ (Mukherjee et al., 1957; Mukherjee and Vickery, 1960) as probably do cultures 6181 of *M. guttatus* and 5865 of *M. nasutus* (Vickery, in press). Of the three tested varieties of *M. glabratus* the local population, 6209 of *M. glabratus* var. *glabratus* has $n = 31$ (Mia et al., 1964), 5063 of *M. glabratus* var. *fremontii* has $n = 30$ (Mukherjee and Vickery, 1960), and 5048 of *M. glabratus* var. *utahensis* has $n = 15$ (McArthur et al., 1972). Thus, *M. wiensii* and *M. dentilobus* form a small complex of taxa with $n = 16$ that is cytologically distinct from the rest of the section except for rather distantly related *M. gemmiparus*.

Detailed morphological comparisons (Table 2) reveal that *M. wiensii* exhibits some traits in common with *M. dentilobus* Robinson & Fernald but is clearly distinct from all the other species of section *Simiolus* as recognized by Grant (1924) and Pennell (1951). In addition, *M. wiensii* shows some similarities with three little-known species not recognized or not included in Grant's monograph or Pennell's treatment. These species are *M. madrensis* Seeman, *M. pennellii* Gentry, and *M. parvulus* Wooton & Stanley. *Mimulus madrensis* Seeman is known only from the type collection, lacks the erose corolla margins that are the hallmark of *M. dentilobus*, and has blunt-tipped leaves in contrast to the pointed, acute leaf tips of *M. wiensii* (Table 2, fig. 1). *Mimulus pennellii* Gentry also is known only from the type collection and has variable, entire to apiculate or slightly erose corolla lobes in contrast to the deeply erose ones of *M. dentilobus* and the entire ones of *M. madrensis* and *M. wiensii* (Table 2, fig. 1). The name *Mimulus parvulus* Wooton & Stanley seems to be a

TABLE 2. CHARACTERISTICS OF THE FOUR SPECIES OF THE *MIMULUS DENTILOBUS* COMPLEX.

	<i>M. dentilobus</i>	<i>M. madrensis</i>	<i>M. pennellii</i>	<i>M. wiensii</i>
Chromosome number	n = 16	?	?	n = 16
Plant habit	prostrate, creeping, forming dense mats (in shade somewhat ascending)	prostrate, ends ascending plants are low, creeping forming dense mats	ascending, creeping forming mats	ascending, forming dense mats
Stem length, cm	1-8	3-14	3-10	5-24
Stem diameter, mm	0.6-1.0	0.2-0.5	0.5-1.0	1.0-1.2
Stem pubescence	glabrous	glabrous	pubescent at the nodes	glabrous, rarely sparsely pubescent
Foliage	light green, rarely darkened with anthocyanin	green	green	usually darkened with anthocyanin
Leaf blades	broadly ovate to sub-orbicular	broadly ovate to sub-orbicular	broadly ovate	ovate to broadly ovate
Leaf blade length, mm	2-10	3-8	3-12	2-20
Leaf blade width, mm	2-9	2-11	2-14	3-13
Leaf surface	not scurfy, scattered punctate glands	crystalline, almost scurfy	slightly crystalline, almost scurfy	punctate, not scurfy

Leaf apex	tending toward blunt	blunt	tending toward acute	often acute
Leaf margins	shallowly sinuate-crenate	shallowly sinuate-crenate	serrate	serrate
Petioles	mostly winged	mostly winged	mostly winged	not winged except near the blade
Leaf venation	lateral veins obscure or the venation reticulate	lateral veins distinct to obscure	lateral veins distinct to obscure	lateral veins typically distinct
Leaf pubescence	glabrous	glabrous	pubescent at the nodes	glabrous, rarely sparsely pubescent
Calyx	slightly accrescent	slightly accrescent	accrescent	accrescent, elongating to as much as 11 mm in fruit
Mature calyx length, mm	5-7	5-7	6-9	7-11
Corolla length, mm	8-14	9-12	8-11	10-14
Corolla lobe margins	toothed to deeply lobed or deeply erose	entire, not apiculate or erose	apiculate to moderately erose	entire, not apiculate or erose
Style	exceeding calyx by more than $\frac{1}{2}$ its length	exceeding calyx by more than $\frac{1}{2}$ its length	exceeding calyx by less than $\frac{1}{3}$ its length	exceeding calyx by less than $\frac{1}{3}$ its length

synonym of *M. dentilobus* and does not refer to a distinct entity. *Mimulus wiensii* does not appear to be within the known range of variation of either of the rare species, *M. madrensis* and *M. pennellii*, or of the better known *M. dentilobus*. These four taxa (*M. wiensii*, *M. madrensis*, *M. pennellii*, and *M. dentilobus*) exhibit enough morphological similarities (Table 2) to suggest that they form a distinctive species complex, the *M. dentilobus* complex. However, the differences among them are sufficiently great to suggest that each should be maintained as a separate species.

The center of distribution for the *M. dentilobus* complex appears to be Sinaloa. Available collections (see above) show *M. dentilobus* to have a broad range from Sinaloa north to New Mexico, east to Texas, and west to Baja California. *Mimulus wiensii* has a smaller range that extends from Sinaloa south to Jalisco and west to Baja California. The other two species apparently are restricted endemics of Sinaloa and the adjacent states to the south.

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THE SUBSPECIES OF LUPINUS CULBERTSONII AND L. CUSICKII (LEGUMINOSAE)

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Polymorphism is especially common in the lupines of the western United States and has long created confusion among taxonomists. By detailed morphological, ecological, and chemical means, small groups of complexes of lupines have been studied by various monographers in efforts to gain insight into the biology of the genus. The following taxonomic treatment of five taxa is an excerpt from an extensive biosystematic study of over 80 described western United States perennial, herbaceous, caespitose lupines (Cox, 1972a). Since these lupines are of special interest in population variation studies, the taxonomic treatments are published here to facilitate later reference to these taxa. On a delineation of morphological traits (Cox, 1972a), it is hypothesized that *Lupinus cusickii* and other related small caespitose lupines are allied to plants that are morphologically similar to *L. culbertsonii*.

The taxonomy is based on comparisons of seed proteins and alkaloids (to be published elsewhere), as well as morphological and field studies conducted during several growing seasons. Chromosome numbers were reported by Cox (1972b). For brevity, complete exsiccatae are not cited here. The following herbaria generously loaned specimens for study: CAS, DS, GH, ISC, JEPS, MIN, MO, NY, ORE, OSC, POM, RM, RSA, UC, UMO, US, WILLU, WIS, WS.

KEY TO THE TAXA

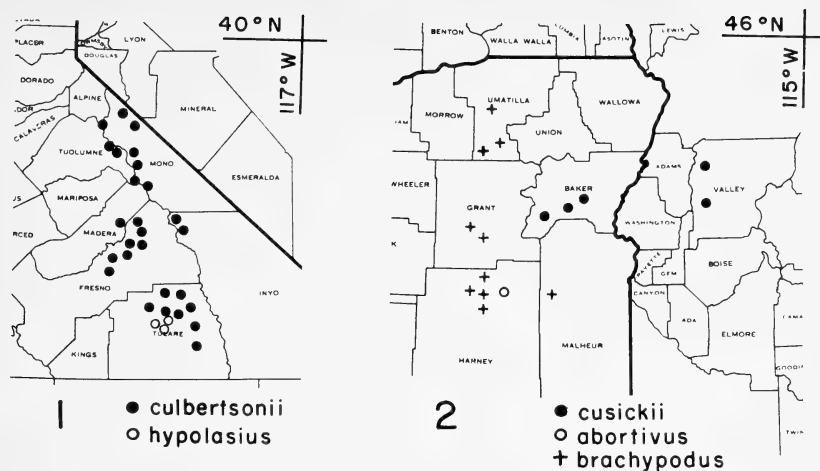
- 1.a. Peduncles surpassing the foliage; plants of the Sierra Nevada, California. 2
- b. Peduncles not surpassing the foliage; plants of eastern Oregon and adjacent Idaho. 3
- 2.a. Stems with 1–2 nodes, branching infrequently; peduncles 8.5–16.0 cm long; along the Kaweah River, Tulare Co.; at 2440–2650 m.
 - 1a. *L. culbertsonii* subsp. *culbertsonii*
- b. Stems with 3–6 nodes, branching frequently; peduncles 1.5–8.0 cm long; from Mono Co. to Tulare Co.; at 2900–3500 m.
 - 1b. *L. culbertsonii* subsp. *hypolasius*
- 3.a. Racemes completely surpassed by the foliage; flowers 8.5–9.0 mm long. 2a. *L. cusickii* subsp. *cusickii*
- b. Racemes not completely surpassed by the foliage; flowers 9.5–11.5 mm long. 4
- 4.a. Plants less than 12 cm tall; leaflets 5–6; stipules 4–5 mm long.
 - 2c. *L. cusickii* subsp. *brachypodus*
- b. Plants usually 12–15 cm tall; leaflets 6–7; stipules 10–15 mm long; Stinkingwater Mt., Harney Co., Ore. 2b. *L. cusickii* subsp. *abortivus*

- 1a. *LUPINUS CULBERTSONII* Greene subsp. *CULBERTSONII*, Leaf. Bot. Observ. Crit. 1:73. 1904. TYPE: United States: California: Tulare Co.: Kaweah River, South Fork, *Culbertson* 4475 (Holotype: ND; Isotypes: MO, NY, POM, UC). — *L. lepidus* var. *culbertsonii* (Greene) C. P. Sm., Bull. Torrey Bot. Club 51:304. 1924.

Plants perennial, foliage in basal clumps from slender woody caudex, branching not prominent in most specimens; stems 15–36 cm tall, 1.5–2.5 mm in diameter, strigose or with sparsely spreading pilose-hirsute pubescence to 2 mm long, acaulescent to 2 cauline nodes; cauline petioles 3–9 cm long; basal petioles 3–8 cm long; stipules 6–9 mm long, adnate to petioles 4–5 mm; leaflets 6–7, oblanceolate, obtuse-rounded to short mucronate, the largest 1.3–2.8 cm long, 5.5–7.0 mm wide, length to width ratio 2.28–4.36 (5.09), av 3.31, sparse sericeous to short pilose-villous, pubescence 1.5–2.0 mm long; peduncles well exceeding the foliage, 8.5–16.0 cm long; racemes 4–9 cm long, 2.5–2.7 cm in diameter, 6–8 verticils, 5–12 mm apart; flowers blue with white to yellow sulcus, 10.2–11.5 mm long; bracts caducous, 4.0–4.5 mm long, subulate, pilose-sericeous; pedicels 2.0–2.7 mm long; calyx bilabiate, upper-lip 4.2–5.0 mm long, bilobed, notch 1.8–2.7 mm deep, lower-lip 4.8–5.8 mm long, tip entire to slightly serrate, lips connate 1.1–1.5 mm, bracteoles persistent, 0.5–1.8 mm long, attached at the sinus to 0.8 mm back, pilose-sericeous, pubescence to 1.5 mm long; banner suborbicular, glabrous, 10.0–10.5 mm long, 7.8–9.0 mm wide, length to width ratio 1.11–1.31, av 1.24, reflexed at or above the midpoint, reflexed to appressed ratio (0.8) 0.92–1.00, angle 121–150°; wings 9.0–10.0 mm long, 5.3–5.8 mm wide, length to width ratio 1.67–1.82, av 1.75; keel 2.8–3.5 mm wide at the widest point, angle 98–106°, sparsely ciliated along the upper-outer half, most dense near the acumen; ovules 4; pods 13–15 mm long, 4.5–5.0 mm wide, subappressed, sericeous-villous; seeds 4, 3.0–3.5 mm long, 2.8–3.0 mm wide, 1.2–1.6 mm thick, beige-tan with darker brown mottlings; flowers late in July–early August; $2n = 48$ (Cox 1972b); (fig. 3).

DISTRIBUTION: This infrequently collected subspecies is endemic to a very small region along the South Fork of the Kaweah River, Kaweah Meadows and Hockett Meadows in Tulare Co., California (fig. 1). It occurs at elevations of 2440–2650 meters.

Plants are morphologically somewhat intermediate between *Lupinus culbertsonii* subsp. *hypolasius* and *L. sellulus*. Flower size and shape, as well as lax, verticillate racemes are traits shared with subsp. *hypolasius*. However, subsp. *culbertsonii* lacks the profuse branching and general spreading pilose to hirsute pubescence common in subsp. *hypolasius*. Instead, it has sparse more or less appressed pubescence, generally has basal leaves, and has long peduncles, common in *L. sellulus*. *Lupinus sellulus* and *L. culbertsonii* subsp. *culbertsonii* are sympatric in the Kaweah region.



FIGS. 1-2. *Lupinus* distributions. 1. Distributions of the subspecies of *L. culbertsonii* in the Sierra Nevada of California. 2. Distributions of the subspecies of *L. cusickii* in eastern Oregon and western Idaho.

1b. *Lupinus culbertsonii* subsp. *hypolasius* (Greene) B. J. Cox, comb. et stat. nov.—*L. hypolasius* Greene, Leaf. Bot. Observ. Crit. 1:74. 1904. TYPE: United States: California: Tulare Co.: Farewell Gap, *Purpus* 5221 (Holotype: ND; Isotypes: MO, UC, US; Photographs: RSA, UMO).

L. brunneo-maculatus Eastw., Leaf. W. Bot. 3:19. 1941. TYPE: United States: California: Mono Co.: Mammoth Crest, Mammoth Lakes, *Rose* 35373 (Holotype: CAS; Photographs: RSA, UMO).

Plants perennial, stems from a thick woody caudex (to 3 cm in diameter), semi-decumbent to erect, few, caespitose to sprawling, lower stems and branches frequently becoming somewhat woody with age, curving at nodes, producing a zig-zag pattern of growth, somewhat fistulose, mostly with secondary branching at each node, 13–27(34) cm tall, 1.0–2.5 mm in diameter, short puberulent-strigose, approaching hirsute, cauline nodes 3–6; cauline petioles 2.5–8.0(10) cm long, on immature plant basal leaves 6–8 cm long; stipules 6–11 mm long, adnate to petioles 3–7 mm, attenuate; leaflets 5–8, oblanceolate-elliptic, acute to obtuse-rounded and mucronate; the largest 12–23(39) mm long, 3.8–6.0 (7.5) mm wide, length to width ratio 2.67–5.42, av 3.71, sericeous to pilose on both surfaces; peduncles 1.5–8.0 cm long; racemes 2–10 cm long, usually 3–5 cm, diameter 19–25 mm, flowers in 2–7 verticils, 5–15 mm apart; flowers fragrant, 10.0–12.2 mm long, blue with white to yellow sulcus; bracts persistent, 4.0–8.5 mm long, subulate-attenuate, pilose; pedicels 2–3 mm long; calyx bilabiate, often minutely gibbous at the

base, upper-lip 4.5–6.4 mm long, bilobed, notch 1.0–2.2 mm deep, lower-lip 5.0–7.0 mm long, entire to serrate, lips connate 1.0–1.8 mm, bracteoles persistent, 0.2–1.0 mm long, attached at the sinus or up to 0.5 mm

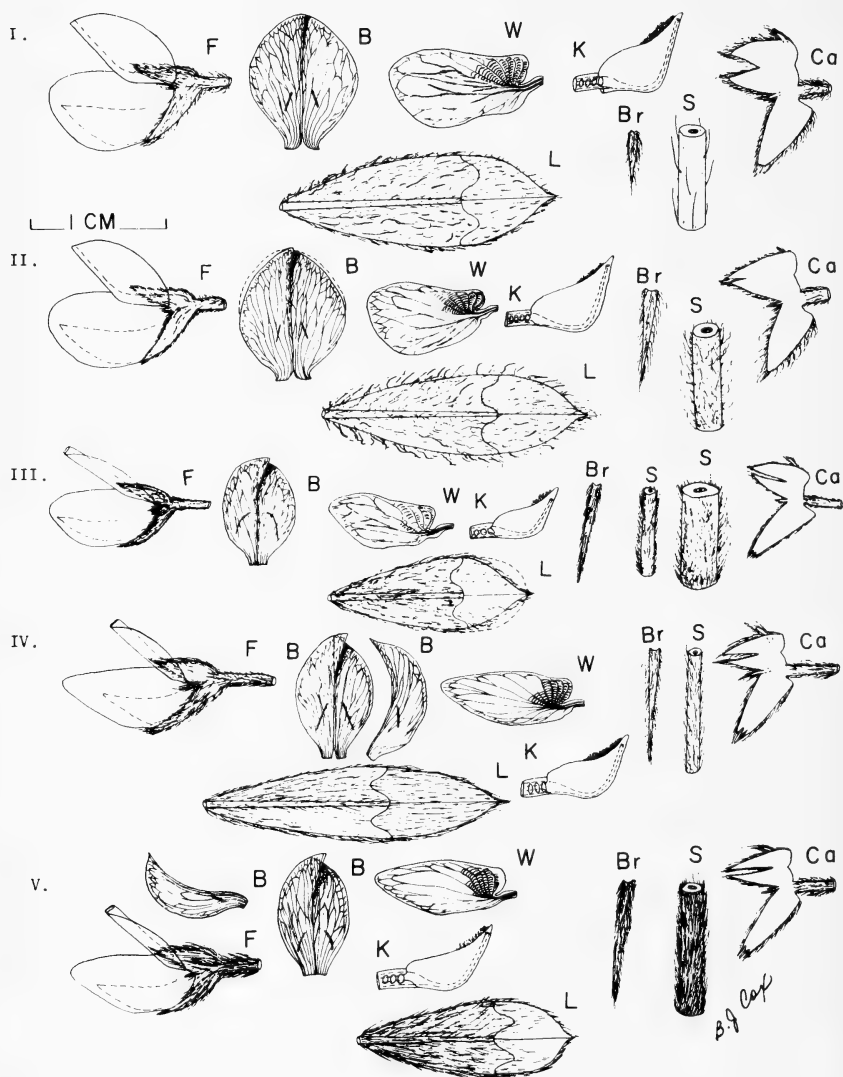


FIG. 3. Floral parts and leaflets of *Lupinus culbertsonii* subsp. *culbertsonii* (I) and subsp. *hypolasius* (II) and *Lupinus cusickii* subsp. *cusickii* (III), subsp. *abortivus* (IV), and subsp. *brachypodus* (V). All parts are drawn to the typical conformation of the structure with the mean value of measurements of a minimum of 25 mature flowers. F = flower; B = banner; W = wing; K = keel; Ca = calyx, inside view, cut open at left lateral sinus; Br = bract; S = stem; and L = av. largest leaflet.

back, strigose-pilose; banner suborbicular to obovate, glabrous, 8.6–10.5 mm long, 6.0–9.3 mm wide, length to width ratio 1.0–1.43, av 1.16, reflexed near the midpoint, reflexed to appressed ratio 0.91–1.20, av 0.99, angle 125–152°; wings 7.9–10.5 mm long, 4.3–6.8 mm wide, length to width ratio 1.44–2.00, av 1.65; keel 2–3 mm wide at the widest point, angle 93–105°, sparsely ciliated along the upper-outer half, most densely near the acumen; ovules 3–4; pods 13–18 mm long, 4.5–5.0 mm wide, densely appressed sericeous; seeds 3–4, 2.6–2.9 mm long, 2.2–2.5 mm wide, 1.1–1.5 mm thick, beige to tan with brown mottling; flowers late July–early August; $2n = 48$ (Cox, 1972b); (fig. 3).

DISTRIBUTION: This subspecies often grows in rather dry sandy or granitic soil among boulders or morainal debris in the Sierra Nevada of California, from Tulare Co. to Mono Co., inclusively (fig. 1). It occupies a subalpine to alpine habitat, normally found at elevations of 2900–3500 meters. Plants are commonly associated with *Pinus murrayana*, *P. albicaulis*, *P. monticola*, *P. contorta*, *Juniperus* sp., *Tsuga mertensiana* and frequently grow at margins of thickets of *Vaccinium* spp.

Although anthesis normally occurs during the latter part of July and first part of August, one collection has been recorded flowering as late as the first of October at 3350 meters elevation on the ridge near Moose Lake, Tulare Co.

The two subspecies of *Lupinus culbertsonii* are morphologically and ecologically distinct. Subspecies *culbertsonii* generally occupies a more mesic habitat than subsp. *hypolasius* and occurs at lower elevations.

The smaller forms of subsp. *hypolasius* tend to resemble *L. lyallii*, the largest forms have traits in common with *L. sellulus* and *L. confertus*, and one specimen has yellow-green leaflets and stems and the shaggy pubescence typical of *L. covillei*. A few specimens in an Inyo Co., Calif., population (Alexander & Kellogg 3329 — GH, MO, NY, RM, UC, US) grow in low mats and have silvery leaves much like *L. lyallii*. Plants from Mono Co. have longer racemes with more verticils than those from elsewhere. Some plants, especially those occurring near Sonora Peak have exceptionally thick woody caudices and stems that are almost entirely glabrous. *Lupinus culbertsonii* subsp. *hypolasius* can be readily identified by the rather large orbiculate flowers in lax, verticillate racemes and by the branching, curving (zig-zag) semi-decumbent stems.

- 2a. *LUPINUS CUSICKII* S. Wats. subsp. *CUSICKII*, Proc. Amer. Acad. Arts 22:469. 1887. TYPE: United States: Oregon: Baker Co.: Forks of Upper Burnt River, *Cusick 1316* (Holotype: GH; Isotypes: MIN, NY, ORE, POM, UC, US; Photographs: RSA, UMO). — *L. aridus* var. *cusickii* (S. Wats.) C. P. Sm., Bull. Torrey Bot. Club 51:303. 1924. — *L. lepidus* subsp. *cusickii* (S. Wats.) Detl., Amer. Midl. Naturalist 45:493. 1951 — *L. lepidus* var. *cusickii* (S. Wats.) Hitchc., Vasc. Pls. Pacif. NW. 3:315. 1961.

L. longivallis C. P. Sm., Sp. Lup. 561. 1946. TYPE: United States: Idaho: Valley Co.: Long Valley, *Henderson 3089* (Holotype: DS, Isotype: US).

Plants perennial with profusely branching, caespitose clumps, 12–30 cm in diameter, 6–12 cm tall; stems 1–3 mm in diameter, from thick, branching, woody caudex, soft, silky appressed pubescent to canescent; each stem with 4–15 cauline nodes; cauline petioles 3–7 cm long, often imbricated at the bases; stipules 5.0–13.5 mm long, adnate to the petiole 3–5 mm, subulate; leaflets 6–9, oblanceolate, acute-mucronate, the largest 8–21 mm long, usually 10–12 mm, width 3–5 mm, length to width ratio 2.67–4.2, av 3.08, densely sericeous-pilose (canescent) abaxially, more sparsely so adaxially to glabrous near the apex and midrib; peduncles 1–2 cm long; racemes 2.0–3.5 cm long, dense, capitate to subcapitate; flowers 8.5–9.0 mm long, blue with yellow sulcus; bracts persistent, 5.5–9.0 mm long, subulate-attenuate, short villous; pedicels 3–4 mm long; calyx bilabiate, upper-lip 4–5 mm long, bilobed, notch 2–3 mm deep, lower-lip 4.5–5.5 mm long, entire to serrate, lips connate 1.2–1.5 mm, glabrous within, subappressed sericeous without, bracteoles persistent, 0.5–1.0 mm long, attached at the sinus to 1.0 mm back, short villous to subappressed sericeous; banner elliptic-suborbicular, glabrous, 7.5–8.0 mm long, 5.0–6.0 mm wide, length to width ratio 1.25–1.60, av 1.40, reflexed below the midpoint, reflexed to appressed ratio 1.13–1.50, av 1.40, angle 160–165°; wings 7.0–8.5 mm long, 3.5–4.0 mm wide, length to width ratio 1.75–2.43, av 2.08, claws 1.5 mm long, glabrous; keel 2.0–2.5 mm wide at the widest point, angle 109–118°, ciliated along the upper-outer half of the margin; ovules 2–3; pods 6–11 mm long, 4–5 mm wide, densely short sericeous to subappressed woolly; seeds 1–3, 3.0–3.2 mm long, 2.2–2.5 mm wide, 1.0–1.3 mm thick, beige; flowers in June and July; $2n = 48$ (Cox, 1972b); (fig. 3).

DISTRIBUTION: *Lupinus cusickii* subsp. *cusickii* is endemic to a narrow region along Burnt River in Baker Co., Oregon, and near Payette Lake in Valley Co., Idaho (fig. 2). The habitat is dry, rocky clay soil in exposed areas that support a depauperate vegetation. The elevation of this habitat is about 1500 meters. Associated plants consist primarily of *Artemisia tridentata* and *Chrysothamnus nauseosus*.

This subspecies bears a superficial resemblance to *Lupinus caespitosus*; however, *L. cusickii* subsp. *cusickii* differs in many traits. Unlike *L. caespitosus*, the stems of subsp. *cusickii* elongate and branch profusely, forming clumps; inflorescences are more or less capitate, appearing at the same level as the leaflets; flowers are generally larger than those of *L. caespitosus*, with reflexed banners, and the entire plant is usually canescent with soft appressed pubescence. Frequently, the leaflets are glabrous adaxially at the apex and sometimes along the midrib, a trait held in common with subsp. *brachypodus*, subsp. *abortivus*, *L. lyallii* subsp. *minutifolius*, and *L. saxosus*, all of eastern Oregon.

Two variant populations of *L. cusickii* in Oregon resemble *L. aridus*

in vegetative patterns. Plants in the Unity Dam population (*Maguire & Holmgren 26732* — GH, MO, NY, UC, US, WS) are approximately 15 cm tall, and are generally somewhat more robust than subsp. *cusickii*. These variants have racemes to 4 cm long, with leaflets to 15 mm long and 5–6 mm wide. The Burnt River population (*Cusick 2543* — GH, MO, NY, ORE, POM, RM, UC, US, WS) consists of plants that are more shaggy, are slightly larger (15–17 cm tall), occur in clumps 15 cm in diameter, have longer cauline petioles (to 9 cm long), have leaflets 20–25 mm long and 6 mm wide, and have internodes more elongated than average.

Plants from Valley Co., Idaho, often have racemes that are more elongated than those of the Oregon populations of this subspecies. On the basis of flower morphology they appear to be referable to subsp. *cusickii* and not to *L. caespitosus* var. *utahensis*, for which they are often misidentified in this geographical region. Although each of these two populations of subsp. *cusickii* is more or less distinctive in a number of traits, their morphological and chemical affinity (Cox, 1972a) to subsp. *cusickii* is sufficiently strong to suggest that they must be included in this subspecies.

Both morphologically and geographically, *brachypodus* and *abortivus* are interpreted as being most closely allied to *Lupinus cusickii*. *Lupinus cusickii* subsp. *cusickii* is generally taller, grows in broader clumps, has smaller racemes and shorter petioles, and is more appressed canescent than subsp. *brachypodus*. Subsp. *abortivus* differs by having elongated racemes that extend up to one-third beyond the foliage. Subsp. *abortivus* is also a larger clumped plant with numerous longer, filiform petioles and stems, and the leaflets are longer and more linear than either of the other two subspecies.

2b. ***Lupinus cusickii* subsp. *abortivus*** (Greene) B. J. Cox, comb. et stat. nov. — *L. abortivus* Greene, *Muhlenbergia* 8:117. 1912. TYPE: United States: Oregon: Harney Co.: Stinkingwater, 1350 meters, 21 Jun 1896, *Leiberg 2353* (Holotype: US; Isotypes: GH, NY, ORE; Photographs: NY, RSA, UMO, US). — *L. aridus* var. *abortivus* (Greene) C. P. Sm., *Bull. Torrey Bot. Club* 51:303. 1924.

Plants perennial, densely caespitose, branching prolifically from a woody caudex into clumps 20–35 cm in diameter, secondary inflorescence branches rise within 3 cm of the base; stems and petioles filiform, height 12–15 cm, stem diameter 1.0–1.5 mm, densely strigose-sericeous to subappressed villous-hirsute; cauline petioles 6.0–9.5 cm long, 2–4 cauline nodes above the 8–10 imbricated basal leaves in the first 3 cm above the branching woody caudex; stipules 10–15 mm long, adnate to the petiole 4–8 mm, subulate-attenuate; leaflets 6–7, oblanceolate-elliptic, acute to slightly mucronate, the largest 14–29 mm long, 4.0–6.5 mm wide, length to width ratio 3.11–6.00, av 4.43, densely short villous on both surfaces; peduncles 1.5–3.5 cm; racemes 3–9 cm, tips exceeding foliage

1–5 cm; flowers densely verticillate, blue to pinkish lavender, 10.0–11.5 mm long; bracts persistent, 7–9 mm long, subulate-attenuate, villous; pedicels 3–4 mm long; calyx bilabiate, upper-lip 4–5 mm long, bilobed, notch 2.0–3.5 mm deep, lower-lip 5.0–6.5 mm long, serrate to tridentate, center tooth 0.3–1.0 mm long, lips connate 1.5–2.0 mm, bracteoles persistent, 0.7–1.0 mm long, attached 1 mm back from sinus, shaggy pubescence; banner oblong-elliptic, glabrous, 8–9 mm long, 4.5–5.5 mm wide, length to width ratio 1.45–1.89, av 1.65, reflexed below the midpoint, reflexed to appressed ratio about 1.7, angle 143–155°; wings, 9.0–10.0 mm long, 4.0–4.5 mm wide, length to width ratio 2.1–2.5, av 2.34, claws 1.5–2.0 mm long, glabrous; keel 2.5–3.0 mm wide at the widest point, angle 107–117°, ciliation from the tip half way back along the upper margins; ovules 2–3; pods 10–13 mm long, 5–6 mm wide, villous to shaggy; seeds 2–3, 2.5 mm long, 2.0 mm wide, 1 mm thick, tan to beige color; (fig. 3).

DISTRIBUTION: *Lupinus cusickii* subsp. *abortivus* is known only from the type collection (fig. 2).

2c. ***Lupinus cusickii* subsp. *brachypodus*** (Piper) B. J. Cox, comb. et stat. nov. — *L. brachypodus* Piper, Bull. Torrey Bot. Club 29:642. 1902. TYPE: United States: Oregon: Malheur Co.: "dry stony bottom of small stream margin of Barren Valley," *Cusick 2561* (Holotype: not located; Isotypes: GH, MIN, MO, NY, ORE, POM, UC, US).

Plants perennial, from a thick woody caudex, 8–10 mm in diameter at ground level, branching to 5–6 tufts of approximately 15 cm in diameter; stems 4–12 cm tall, 1–2 mm in diameter, densely strigose to ascending short villous-hirsute pubescence; cauline petioles 2–5 cm long, cauline nodes 1–3; leaves mainly basal, basal petioles 1.5–7.0 cm long; stipules 4–5 mm long, adnate to petioles 1–3 mm, small subulate; leaflets unequal, 5–6, oblanceolate-elliptical, acute, the largest 10–18 mm long, 5–6 mm wide, length to width ratio 2.4–3.1, av 2.8, densely sericeous to villous-hirsute abaxially, more sparsely so adaxially, greener above; peduncles 2–4 cm long; racemes 2.0–5.5 cm long, 2.0–2.3 cm in diameter, usually at the level of the leaflets, not exceeding the foliage by more than 1–2 cm; flower arrangement densely subverticillate; flowers 9.5–11.0 mm long, generally 10 mm long, blue to pinkish with a white sulcus; bracts persistent, 6.5–7.0 mm long, attenuate-subulate, pilose-sericeous to villous; pedicels 2.5–3.5 mm long; calyx upper-lip 4.5 mm long, bilobed, notch 2.5–3.0 mm deep; lower-lip 5.0–5.5 mm long, deeply serrate to tridentate, the center tooth 0.3–1.0 mm long, lips connate 1.5 mm, bracteoles persistent, 1.0–1.5 mm long, sericeous to villous, attached at the sinus; banner elliptical, glabrous, 8–9 mm long, 4.5–6.5 mm wide, length to width ratio 1.38–1.78, av 1.65, not reflexed or semi-reflexed forming approximately 160° angle, wings 8–10 mm long, 3–4 mm wide, length to width ratio 2.29–2.83, av 2.50, claws 1.5–2.0 mm long, gla-

brous; keel 2.0–2.5 mm wide at the widest point, angle 108–118°, ciliated along the upper margin from the acumen to half the distance back; ovules 2–3; pods 10 mm long, 5 mm wide, silky-villous to woolly; seeds 2–3, 2.5 mm long, 2.0 mm wide, 1.0 mm thick, beige to tan color; flowers in mid-June; (fig. 3).

DISTRIBUTION: *Lupinus cusickii* subsp. *brachypodus* has been collected only in eastern Oregon in Grant, Harney, Malheur, and Umatilla counties (fig. 2). The plants are found primarily in arid, rocky stream beds and on mountain ridges. They do not occur in abundance, and they have been collected infrequently. Associated plants are predominantly *Artemisia* spp. and *Chrysothamnus* spp.

Subspecies *brachypodus* generally has capitate racemes like subsp. *cusickii*, but the flowers are larger, approaching the size and shape of those of *L. aridus*. The vegetative height and general stature of subsp. *brachypodus* resemble *L. caespitosus* var. *utahensis*, but *utahensis* usually has elongated, narrower racemes and smaller flowers than the former. The petioles of subsp. *brachypodus* are mainly basal, unlike the cauline leaves of *L. caespitosus* var. *utahensis*. Although the raceme diameter and flower size of subsp. *abortivus* approximate those of subsp. *brachypodus*, the former has elongated racemes that surpass the foliage by 1–5 cm, forming larger clumps with more filiform stems and petioles.

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FURTHER EVIDENCE FOR THE SYSTEMATIC POSITION OF PSITTACANTHUS SONORAE (LORANTHACEAE)

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The Mexican mistletoe *Psittacanthus sonorae* (S. Wats.) Kuijt has recently been transferred to *Psittacanthus* from *Phrygilanthus* on the basis of a single character (Kuijt, 1971). This character, the absence of endosperm in the mature seed, is in Loranthaceae unique to *Psittacanthus*, at least under the current circumscription of neotropical genera. I should like to further substantiate this taxonomic transfer by means of some observations on the fruit and seedling. These observations, furthermore, include a number of details in which *P. sonorae* differs from other known *Psittacanthus* species; some of these details seem to represent adaptations to the extremely xerophytic environment of the Sonoran Desert. A comparative basis has been provided by my two earlier articles on *Psittacanthus* (Kuijt, 1967 and 1970).

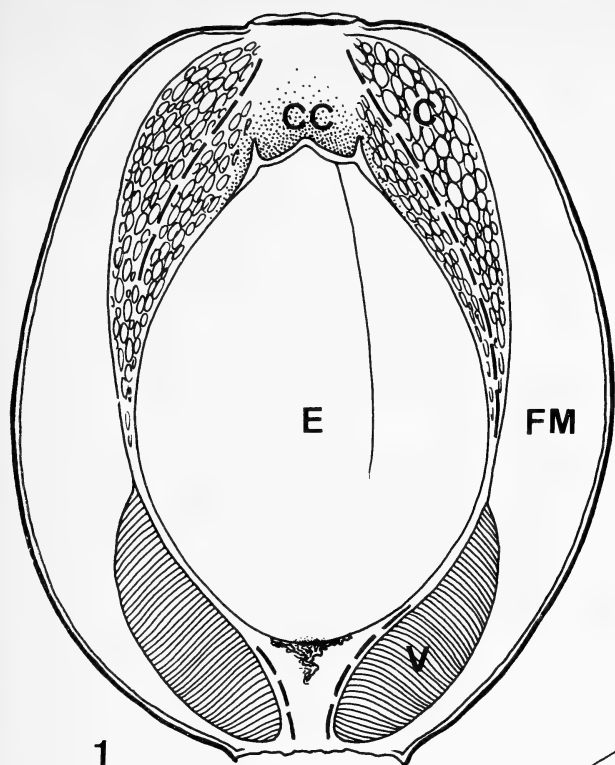
The materials for this study were gathered by Dr. P. D. Warrington and me about 5 km north-west of Bahia de los Angeles, Baja California, 8 Jan 1968. All individuals seen were parasitic on *Bursera*, the plants here described growing on *B. microphylla* A. Gray.

FRUIT

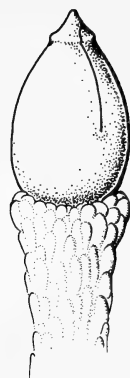
The mature fruit is nearly spherical and about 7 mm in diameter. It is shiny and smooth, and dark purple or black. A longitudinal section reveals the main details of its complex inner structure (fig. 1). The outer tissues, including the fleshy part of the mesocarp layer, slip off with remarkable ease. The proximal region of the fruit includes a very thick and rigid layer of large, hyaline cells that are light brown. This tissue is referred to as the *capsule* for reasons that will become clear below. The axial region, however, is occupied by a strong, persisting "collenchymatous cup" that seems to function as a barrier or receptacle to the descending embryo (and, in other genera, endosperm; Maheshwari et al., 1957). Six vascular bundles can be traced through the middle of the capsular tissue and around the embryo to the scars of the petals. As will be seen below, the capsule functionally is comparable to the testa. Morphologically, however, it represents the endocarp; as in other Loranthaceae, a true testa is absent. Distally, a funnel-shaped mass of viscid tissue adheres tightly to the seed. Its cells are greatly elongated in a radial direction, and are of a clear, blue-green color. The viscid tissue probably should be counted with the mesocarp, as is indicated by a comparison with another species, *P. schiedeana* (Cham. & Schlecht.) Blume (Kuijt, 1967).

The central portion of the fruit is occupied by a single, ovate, fleshy embryo (fig. 2). The cotyledons make up about half of its bulk. Most embryos have two cotyledons, but some with three may also be found. Furthermore, even in those with two cotyledons much variation in cotyledon size occurs; one cotyledon is often two or three times as large as its mate (fig. 3). The apex of the larger of the two is pressed tightly into the collenchymatous cup and consequently bears the latter's nipple-like imprint. A colorless, thin tissue invests the very base of the embryo and is attached to it (fig. 2). It is the compressed remnant of the massive suspensor that characterizes the embryogeny of *Psittacanthus* (Kuijt, 1967). In a fruit that is about half mature this remarkable suspensor can still be seen as a stout, translucent stalk made up of very large cells

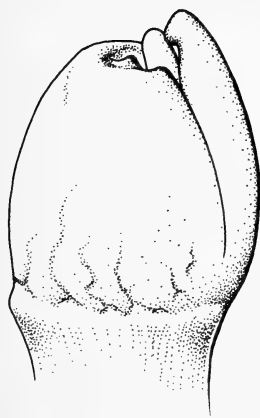
FIGS. 1-4. 1. Longitudinal section of mature fruit, the scar of the peduncle being above. $\times 13$. C. Capsule, the broken lines representing vascular bundles. CC. Collenchymatous cup. E. Embryo, with suspensor remnant basally attached. FM, Fleshy mesocarp. V. Viscin. 2. Mature, dicotyledonous embryo and suspensor remnant, dissected from a ripe fruit. $\times 13$. 3. Top of a young seedling, the capsule removed, showing a young leaf pushing aside the smaller (right) of two very unequal cotyledons. $\times 6.5$. 4. Young dicotyledonous embryo and upper portion of suspensor dissected from a semi-mature fruit. $\times 13$.



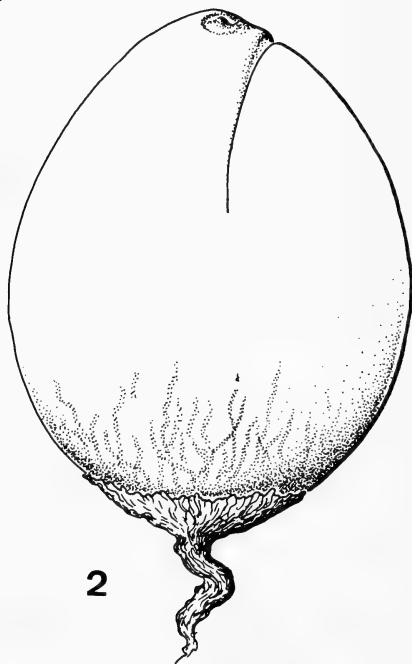
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(fig. 4), pressing the embryo against the collenchymatous cup. Subsequently the expanding embryo compresses and obliterates the suspensor. The embryo lacks green coloration, and is light cream-colored throughout except for series of red-pigmented epidermal cells at the base (fig. 2).

GERMINATION

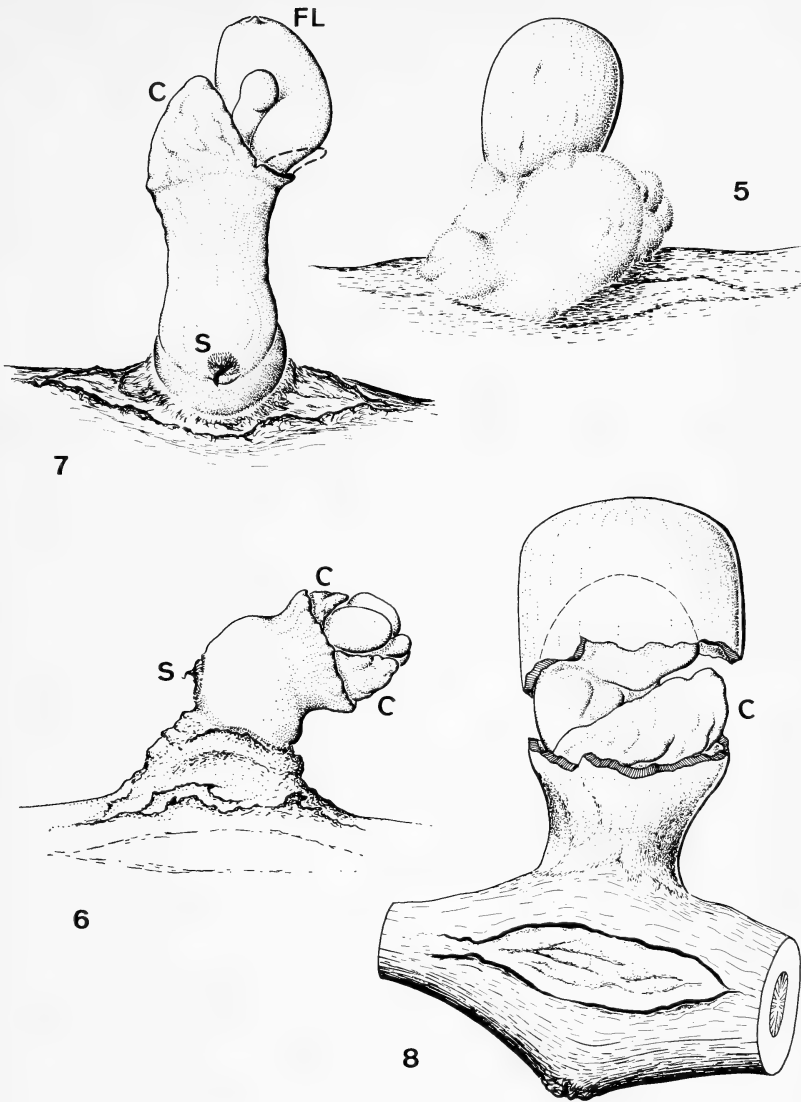
The seed adheres to the host twig in such a way that the radicular pole is nearest the host surface, a position probably due to the presence of viscid tissue at that end. The most common position of a germinating seed is thus with the cotyledonary end tilted obliquely upward (figs. 5 and 6). The associated capsular layer and the viscid tissue now dry up and apparently seal off the seedling from the air. The former tissue persists as a rigid capsule, the latter as a much more elastic, sleeve-like envelope.

The cotyledons do not, as in other *Psittacanthus* species, spread immediately. In fact, they do not spread at all in the normal sense of the word, but are forced apart by the young leaves much later. The haustorium apparently forms very early. That it originates from the lower flanks of the embryo and not from its apex is clearly demonstrated in established seedlings, where one can always observe the suspensor scar or remnant that has been pushed to the side (S in figs. 6, 7, and 9). A small, smooth haustorial cushion develops just external to the host (fig. 7). In older seedlings irregular, globular swellings lower down indicate the growth of the haustorium, which, as in other species of the genus, can become very massive. *Bursera* twigs, where attacked by *P. sonorae* seedlings, often exude gum copiously, in extreme cases investing the base of the seedling completely (fig. 5). A comparison of the mature embryo and established seedlings shows that the lower half of the embryo elongates somewhat during haustorial formation, but also that it becomes thinner (cf. figs. 2 and 7).

When the seedling is securely established the cotyledons, which until now have been tightly appressed to each other, are forced apart by one to several young leaves (figs. 2, 6, 7). The cotyledons at this stage are wrinkled and obviously shrunken. As their color is now a dull, light brown they may no longer contain living tissues. The zone where hypocotyl and cotyledons meet does not shrink as much as the tissues above and below, and thus often stands out as an elevated collar (fig. 6).

The emerging young leaves push against the inside of the rigid capsule that surmounts the seedling until the capsule separates by means of an irregular, transverse tear from the viscid "sleeve" below (fig. 8). Further elongation of the leaves completely lifts off the capsule and causes it to be dropped. Thus the cotyledons are exposed only when they are no longer functional as storage organs, and at a time when haustorial establishment is already secure.

The leaves that push off the capsule are not, however, morphologically the first foliar organs of the plumule. In all germinating seedlings a



FIGS. 5-8. 5. Seedling in natural position, its base enveloped by host gum. $\times 5$. 6. Dicotyledonous seedling with capsule and viscin removed. $\times 6$. C. Cotyledons, between which the expanding leaves. S. Suspensor remnant, pushed aside by the expanding haustorial organ below. 7. The same seedling as that in Figure 8, seen from the opposite side, with capsule and viscin removed. The broken line indicates one small cotyledon which had apparently aborted. $\times 7.5$. C. Cotyledon. FL. Foliage leaf. S. Suspensor remnant, below which the smooth haustorial cushion. 8. Young seedling in which one foliage leaf is in the process of pushing up and rupturing the capsule. The sleeve of viscin tissue is below the line of rupture. The swelling of the host branch shows the haustorium to be fully established. $\times 7.5$. C. Cotyledon.

zone of various numbers of extremely reduced leaves separates the cotyledons from the youngest expanded leaves. In some seedlings these organs are few or are reduced to such a degree as to be scarcely discernible. In others a small central prominence and surrounding leaf cushion is set apart from adjacent, similar organs. In the clearest instances such a leaf cushion is surmounted by a minute, awl-shaped leaf (fig. 9). An uninterrupted gradient of these reduced leaves may be observed when studying many seedlings. In any one seedling, however, an abrupt transition exists between reduced and normally expanded leaves. That even the smallest of these organs are, morphologically, leaves is confirmed by the occasional emergence of lateral branches in their axils. An older plant may therefore have lateral branches in positions that appear to be below the first foliage leaves, especially when the main axis has been injured.

DISCUSSION

The above observations on embryogeny, fruit structure, and germination of *Psittacanthus sonora* demonstrate that, in the main, these features are similar to those in the other species of *Psittacanthus* that have been investigated (Kuijt, 1967 and 1970). The mature fruit has no recognizable endosperm. The proembryo and suspensor develop conjointly, the proembryonic cell group at one time being no more than a minute distal portion of the massive suspensor. Gradually the embryo enlarges and differentiates, and eventually crushes the suspensor completely. A fully developed embryo bears only a remnant of the suspensor at its radicular pole. The presence of this tissue remnant implies that, in this precise locality, no truly terminal primary haustorium can be formed as in other advanced Loranthaceae. The haustorium, therefore, originates on the lower flanks of the radicular end of the seedling, and in time pushes the suspensor scar or remnant aside. This extraordinary developmental sequence, so far known only from *Psittacanthus* but conceivably also present in some other South American Loranthaceae, may well provide a firmer systematic foundation for the genus than the mere absence of endosperm associated with it. At any rate, the generic allocation of this species to *Psittacanthus* now appears to be beyond question.

Another feature that may characterize *Psittacanthus* as a whole is the variation in form and number of cotyledons. As detailed earlier (Kuijt, 1967), the species of this genus may have as many as eleven cotyledons. In one instance (*P. allenii* Woods. & Schery) what appears to be a single species is characterized by two flat cotyledons in one area of Costa Rica, and by numerous prismatic cotyledons in a different area of the same country (Kuijt, 1970). In *P. sonora* a certain amount of variation also occurs, but even more interesting is its loss of photosynthetic function.

It may well be that the cotyledonary variation in *Psittacanthus* stands in some relation to its remarkable embryogeny or to the disappearance of the endosperm. It is as if the conjoint suspensor-embryo development,

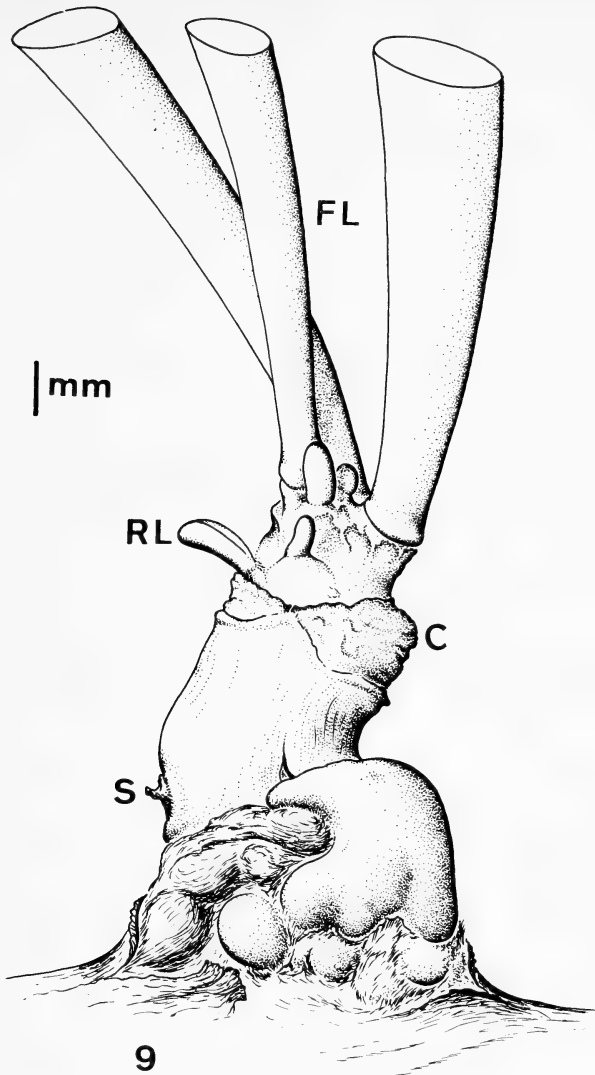


FIG. 9. Older seedling, showing irregular growth of haustorium below. C. Cotyledon. FL. Expanding foliage leaves. RL. Rudimentary leaves. S. Suspensor remnant.

or the loss of the endosperm, has somehow weakened the morphogenetic control over cotyledon number and shape. It is interesting to find, in this context, that cotyledon number in at least some normally dicotyledonous plants is amenable to a certain amount of experimental manipulation (Haccius and Reinholz, 1953).

Although small percentages of polycotyledonous seedlings occur in a great variety of normally dicotyledonous plants (Haccius, 1955), the

number of species for which polycotyledony is the rule is exceedingly small. *Bruguiera* (Rhizophoraceae) is characterized by four cotyledons, and the number ranges from two to eight in *Persoonia* (Proteaceae), as reported by Goebel (1932). A few species of *Navarretia* (Polemoniaceae) normally have either three or four cotyledons (Brand, 1907). Finally, in several New Zealand species of *Pittosporum* (Pittosporaceae) three or four cotyledons are usual (Stebbins, 1972). As this sort of information is difficult to recover from the scientific literature I may well have overlooked other instances. It would be interesting to know if any unusual features in the embryogeny are associated with polycotyledony in the species listed, comparable to those of *Psittacanthus*.

The formation of rudimentary leaves as first foliar organs above the cotyledons has also been mentioned and illustrated for *P. allenii* (Kuijt, 1970). In the latter species, however, the rudimentary leaves are very few and difficult to discern, and transitional leaf-forms do not seem to occur. Their greater number and prominence in *P. sonora* is perhaps related to the time-lag in plumular differentiation as mentioned below.

In spite of the above-mentioned structural correspondence between *P. sonora* and its fellow species, there are also some significant differences. First of all, *P. sonora* may be the only *Psittacanthus* species in which the cotyledons do not spread immediately and are not photosynthetically active. Secondly, compared with the fruit of *P. schiedeana* (Kuijt, 1970), the *P. sonora* fruit has a viscid zone that is histologically very distinct from the fleshy part of the fruit wall, their contact zone being a separation layer. Thirdly, the inner fruit wall is strongly developed in *P. sonora*, particularly at the cotyledonary end of the embryo, and dries into a hard shell or capsule surrounding that part of the seedling. Finally, the development and expansion of normal foliage leaves appears to lag far behind haustorial establishment. The reduced leaves mentioned earlier may indicate a degree of meristematic activity of the plumular apex during haustorial formation. There is little question that the presence of the protective capsule, aided by the viscin tissue and perhaps even the gum exudates from the host, is of great ecological advantage during the early phases of germination. The delayed foliar expansion extends the duration of this adaptive feature by keeping the capsule intact until the haustorial connection is fully functional.

SUMMARY

The structure of the fruit and seedling of the Mexican mistletoe *Psittacanthus sonora* (S. Wats.) Kuijt (Loranthaceae) confirms its generic position. Differences from other species of *Psittacanthus* are to be found in the non-chlorophyllous cotyledons, which do not expand normally, and particularly in the capsule-like differentiation of the endocarp, providing extended protection for the young seedling. The first expanding foliage leaves rupture the base of the capsule at a time that the haustorium is fully established.

ACKNOWLEDGMENTS

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MORPHOLOGY, FLAVONOID CHEMISTRY, AND CHROMOSOME NUMBER OF THE CHENOPODIUM NEOMEXICANUM COMPLEX

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The genus *Chenopodium* is generally recognized as very difficult taxonomically. Often it is almost impossible to circumscribe species with certainty because no sharp morphological discontinuities appear to exist in particular groups or complexes of plants. This paper represents the first of a series that will be devoted to the systematics of western North American species of *Chenopodium*. The investigations will utilize flavonoid chemistry, field studies of natural populations, micromorphology, chromosome numbers, and morphology.

This report is concerned with the results of a study of a group of triangular-leaved, attached-pericarp chenopods that are restricted to Arizona, New Mexico, Texas, and northern Mexico, here referred to as the *Chenopodium neomexicanum* complex. They occur typically in disturbed, weedy roadside habitats in mountains above 1650 m elevation. Individuals apparently are not common; collections in herbaria are few, and I have had some difficulty in locating plants in the field.

Chenopodium neomexicanum was described by Standley (1916) in

his treatment of Chenopodiaceae for the North American Flora. In the same publication, he proposed three additional species, namely, *C. palmeri*, *C. arizonicum*, and *C. parryi*. Standley distinguished these four taxa on the basis of such characters as seed size, length of leaf blades, shape of leaf apices (rounded vs. acute), odor of the plants, and whether the plants were upright vs. spreading from the base.

Aellen (1929) described *Chenopodium lenticulare*, a species closely related to the taxa previously erected by Standley. Aellen concluded that *C. parryi* was synonymous with *C. arizonicum*, and he also made *C. palmeri* the basis of the new subspecies *eu-berlandieri* of the species *C. berlandieri*. Why Aellen did not take up the name *palmeri* for this new taxon is not clear. Aellen alluded to *C. neomexicanum* as being a member of this complex of species, but he neither recognized it formally nor placed it in synonymy. He simply placed a question mark after the name, which I take as an indication that he was unsure of its proper placement.

The treatment of this group by Aellen and Just (1943) was the same as that of Aellen (1929) except they placed *C. neomexicanum* under *C. watsonii* forma *glabrescens*. Apparently Aellen had decided on this placement shortly after his 1929 manuscript had gone to press. The type specimen bears his annotation (1929), indicating that he chose to recognize the taxon at the varietal level instead of as a forma. This combination was never published.

Wahl (1952-53) recognized *C. palmeri* as a species and treated *C. arizonicum* as a synonym of it. He thus did not accept the ideas of Aellen (1929) and Aellen and Just (1943) that *C. palmeri* belongs with *C. berlandieri*. I consider this to be a very fundamental difference in interpretation. Wahl treated *C. neomexicanum* as distinct from *C. watsonii* f. *glabrescens*, and he placed *C. lenticulare* under the former. Wahl's concept of species in *Chenopodium* is clearly different from those of previous workers. He makes no mention of *C. parryi*.

Reed (1969) agreed with Wahl that *C. neomexicanum* and *C. lenticulare* are synonymous. He does not concur with Wahl's recognition of *C. palmeri* as a distinct species. Instead, he agrees with Aellen (1929) and Aellen and Just (1943) in placing the species under *C. berlandieri*. Reed also considers *C. arizonicum* to be the same as *C. palmeri*, and thus likewise puts it with *C. berlandieri*. In essence, then, he agrees with Wahl that both *C. palmeri* and *C. arizonicum* are the same, but he feels that they are not distinct from *C. berlandieri*.

Clearly, workers have held and continue to hold widely divergent views on the taxonomy of these chenopods. The purpose of the present study was to answer the following questions: (1) How many species should be recognized within the so-called *Chenopodium neomexicanum* complex? (2) Are any or all of the taxa in the *C. neomexicanum* complex distinct from *C. berlandieri*? (3) What are the relationships of the *C. neomexicanum* complex within the genus?

MATERIALS AND METHODS

Field collections and observations were made during the late summers of 1971 and 1972. When available, at least five plants were collected from each population.

Fruits were measured to the nearest 0.05 mm utilizing a dissecting microscope with an ocular micrometer. Ten determinations were made for each plant, and the mean was taken as the value for the individual.

For the epidermal studies, leaves were cleared in 5% sodium hypochlorite followed by 25% chloral hydrate. They were then dehydrated in an ethyl alcohol-xylene series, and mounted in balsam.

For the chromosomal studies, root tips from germinating seeds were pretreated with 0.2% aqueous colchicine for four hours before fixation in ethyl alcohol: acetic acid (3:1 v/v). The fixative was washed out with several changes of 70% ethyl alcohol. Chromosomes in the dividing cells were stained using the alcoholic hydrochloric acid-carmin technique as described by Snow (1963).

Flavonoid compounds were extracted from the plants by eluting them in absolute methanol for 24 to 48 hours. All parts of the plants contained the same flavonoids, and thus whole plants were used. The compounds were separated by two dimensional chromatography using 46 x 57 cm sheets of Whatman 3 MM paper. The procedures employed for the determination of chromatographic profiles and the identification of individual compounds are standard ones (Mabry, Markham, and Thomas, 1970; Crawford, 1973). In all instances at least two plants from each population sample collected by the author were analyzed chemically to check for intrapopulation variation. When sufficient material was not available for paper chromatography (collections other than those of the author), flavonoid profiles were determined on thin layer plates coated to a thickness of 500 μ with avicel-ph-101 microcrystalline cellulose.

All specimens, except the types, which are in US, are deposited in RM.

RESULTS

Morphology. Standley (1916) employed leaf blade length as a taxonomic character, and used it for distinguishing between *C. palmeri* and *C. arizonicum*. My studies indicate that this feature is rather constant and similar in these plants, if comparable leaves are considered. The most important factor influencing size of the blades on a particular plant is the degree of maturity of the individual. The first leaves to develop along the central stem (the primary ones) are larger than any that appear later. These leaves are also the first to fall from the plant. Secondary leaves develop on side branches that come from the axils of primary leaves. Reduced bractlike leaves are produced on the upper part of a plant, both directly below and as a part of the inflorescence. The important point is that there are no consistent differences in leaf size between plants, if comparable leaves are considered. Plants fall into two groups on the basis of leaf blade length (fig. 1). It is of interest to note, however, that

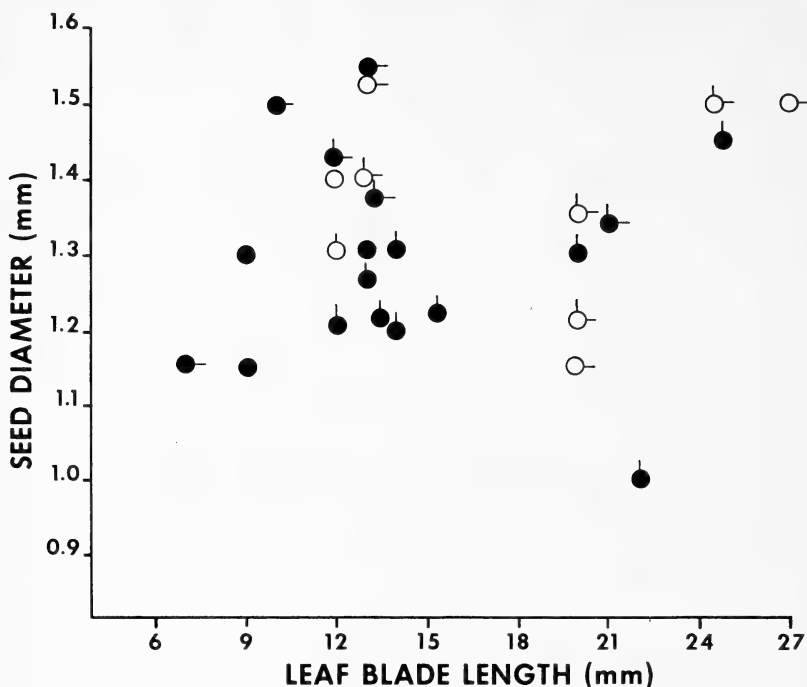


FIG. 1. Pictorialized scatter diagram depicting characters of individual plants in the *C. neomexicanum* group. Open circles represent plants that are basically upright, whereas closed circles indicate basally-branching individuals. Horizontal arms depict plants with leafy inflorescences, and the absence of arms indicates leafless or nearly leafless inflorescences. Vertical arms show plants with bipartite basal lobes on the leaves, the absence of such arms represents plants with leaves having entire basal lobes.

those individuals with the smaller leaves are quite mature and bear only secondary leaves. By contrast, the plants with the larger leaves are less mature and still have the primary ones present.

Standley (1916) considered the nature of the leaf apex (rounded vs. acute) to be of taxonomic significance. Current investigations show that this feature, like leaf size, depends to a large degree on whether a leaf is a primary, a secondary, or a reduced upper one. A rounded apex is characteristic of most primary ones, whereas acute apices occur on secondary and bractlike leaves. This can be demonstrated by studying plants in which all types of leaves are present (fig. 2).

The presence or absence of bipartite basal lobes on leaves has been used as a diagnostic character in this group (Wahl, 1952-53). My data indicate that this feature is quite variable and is not correlated with other characters (fig. 1). Field investigations show it to be variable at the intrapopulational level.



FIG. 2. Silhouettes of primary, secondary, and upper reduced leaves from an individual plant of *C. neomexicanum*.

The leaves of all plants within the *C. neomexicanum* complex are similar in that they are basically triangular in shape with lobes at or near the base. The margins above the basal lobes are invariably entire (fig. 3A,B). By contrast, the leaves of *C. berlandieri*, while somewhat variable in shape, are not basically triangular, and they have no pronounced basal lobes. In addition, the margins are variously toothed above the base (fig. 3C—E). Although these differences are not striking, they are consistent.

Two other morphological characters that have been used in the *C. neomexicanum* group are whether the plants are basically upright vs. spreading from the base with well developed branches and the degree of leafiness of the inflorescences. I have found it impossible to apply either feature with any degree of consistency. Neither character is correlated with other morphological features (fig. 1), and both are variable within individual populations. Also, it is of interest to note that the type sheet of *C. lenticulare* contains one plant that is strongly upright, whereas the other individual is freely branched from the base.

Standley (1916) considered *C. parryi* to be the only foul-smelling species of this complex. Aellen (1929) indicated that all taxa have a bad odor. Current studies of fresh and crushed dried material show that none is fetid. The only taxa that are truly malodorous are *C. watsonii* and *C. glabrescens*, both of which will be treated in a later paper.

Fruit size and shape are usually consistent features within species of *Chenopodium*, and many authors have used them as a basis for separation of species within this complex. Present investigations indicate that this is not feasible within the *C. neomexicanum* group. The fruits vary from 1.0 to 1.55 mm in diameter, and there are no gaps nor discontinuities in the variation pattern (fig. 1). In addition, no other characters are consistently associated with plants that have fruits of a particular size. Measurements of fruits from different plants from several populations have revealed that fruits may vary from 1.10 to 1.40 mm in diameter

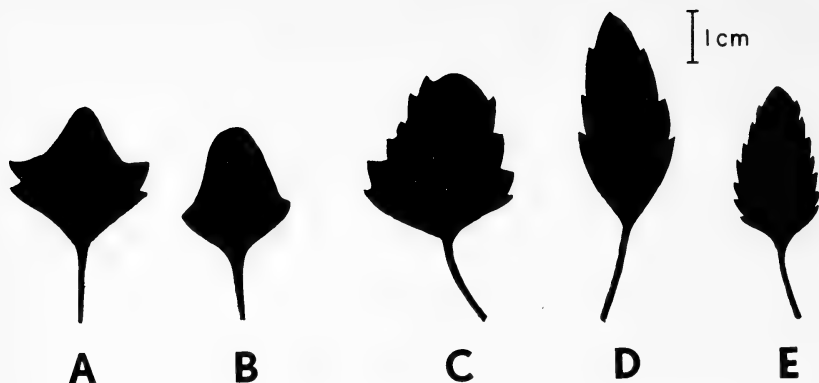


FIG. 3. Silhouettes of primary leaves of *Chenopodium*. A-B of *C. neomexicanum*; C-E of *C. berlandieri*.

within a population. Whether the margin is obtuse or rounded vs. acute is likewise extremely variable at the intrapopulation level and is impossible to apply as a taxonomic character.

Fruits of *C. berlandieri* have a conspicuous yellow area (appearing light in color) at the base of the persistent styles whereas those of the *C. neomexicanum* complex never display this feature (fig. 4). This character of *C. berlandieri* fruits was mentioned by Wahl (1952-53), and I have found it to be reliable for separating this species from the *C. neomexicanum* complex.

In members of the *C. neomexicanum* group the sepals are strongly spreading at maturity and wholly expose the fruits. By contrast, the sepals of plants of *C. berlandieri* are never strongly spreading and do not expose the fruit to a very large degree (fig. 4).

Leaf Epidermis. The lower leaf epidermis was examined from plants from six populations belonging to the *C. neomexicanum* group. Three leaves from two different individuals of each population were observed. The epidermal cells have straight walls, and the guard cells range in size from 15 to 25 μ (fig. 5A). This range of sizes was found on individual leaves, and was not associated with different leaves on the same plant, different plants from the same population, nor plants from different populations. The mean length for all guard cells measured (over 200) was 21 μ .

An examination of the lower leaf epidermis from ten plants of *C. berlandieri* has shown that the pattern is similar to that found in the other group, but the epidermal and guard cells are consistently larger (fig. 5B). The range in guard cell length is 25 to 35 μ with the mean from the 100 cells examined being 30 μ .

Chromosome Numbers. Chromosome numbers were determined from germinating seeds from three different populations (Arizona, Apache

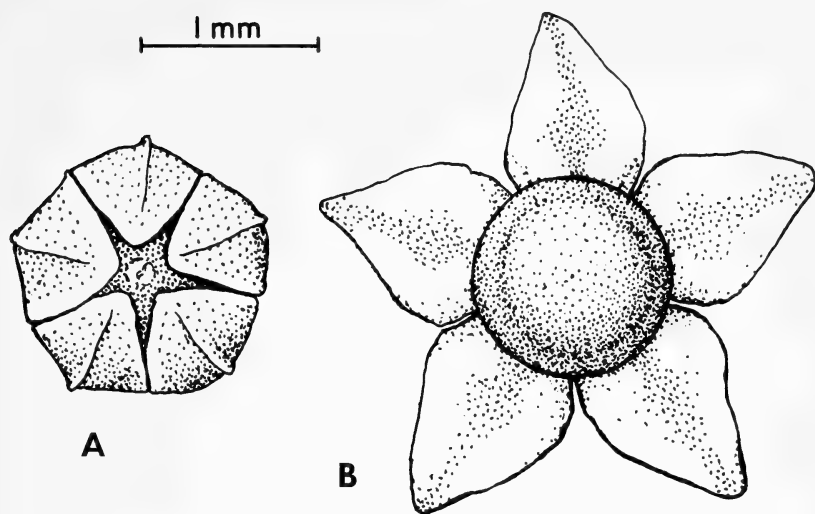


FIG. 4. Fruits and sepals of *Chenopodium*. A, *C. berlandieri* with enclosing sepals and light (actually yellow) area around the style base on the fruit; B. *C. neomexicanum* with spreading sepals that expose the fruit.

Co., ca 5 mi W of Springerville, *Crawford* 522; New Mexico, Grant Co., 12 mi S of Silver City, *Crawford* 722; 9 mi S of Silver City, *Crawford* 727). All determinations proved to be $2n = 18$, and these agree with the one previous report (Keener, 1970) (Arizona, Pima Co., *Wahl* 21826.) Whereas little chromosomal information has been available for the *C. neomexicanum* group, there are several reports for *C. berlandieri* (Bassett and Crompton, 1971; Homsher, 1963; Keener, 1970; Mulligan, 1961); all tetraploid $2n = 36$.

Flavonoid Chemistry. Thirty individuals belonging to the *C. neomexicanum* group were examined for flavonoid constituents. The profiles for all of these plants are extremely uniform and are quite simple. All show two 3-*O*-glycosides of the flavonol quercetin; one is the rutinose and the other is a rhamnoglucoside. It should be emphasized that extracts from the type specimens of all species in this group yielded profiles on thin layer plates that appeared identical to each other. In addition, these patterns corresponded to those obtained on paper in which extracts from my own collections were used.

The flavonoid constituents of *C. berlandieri* differ from those of the *C. neomexicanum* complex. The two share quercetin 3-*O*-rutinose, but differ in other components. Spectral studies show that both produce only quercetin but the R_f values of the compounds demonstrate that, except for the rutinose, the sugars attached to the quercetin nucleus differ in the two. Over ten collections of *C. berlandieri* were studied chemically, and the difference between the profile of this species and that of the other group is consistent.

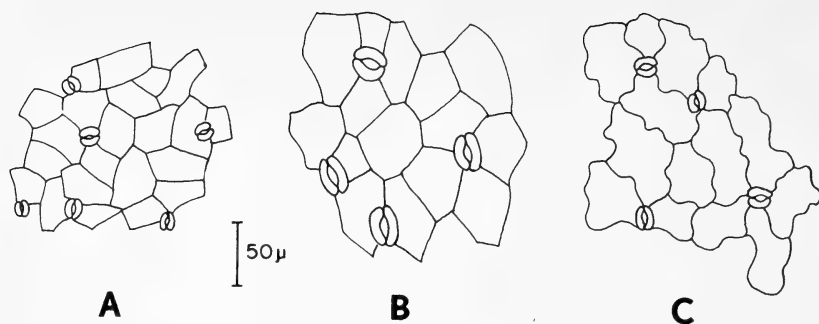


FIG. 5. Camera lucida drawings of the lower leaf epidermis of *Chenopodium*. A, *C. neomexicanum*; B, *C. belandieri*; C, *C. fremontii*.

DISCUSSION AND CONCLUSIONS

The present study has demonstrated that morphological features that have been employed for distinguishing the five "species" in the *C. neomexicanum* group are not consistent. Additionally, the combinations of characters that have been alleged to circumscribe taxa indeed do not occur (fig. 1). Previous workers, particularly Standley (1916), picked individual plants that exhibited certain features as the types for species. The distinctive characters of these plants are the result primarily of their maturity and do not reflect genetic differences. For example, the holotype of *C. arizonicum* is an extremely mature plant with all primary leaves missing and only secondary and bract-like ones remaining. By contrast, the type specimen of *C. palmeri* is a much less mature individual with primary leaves intact. It is obvious that the "key" characters used by Standley to separate the two taxa, i.e., leaf length and apex shape, reflect this difference in maturity.

Collections and field studies have shown that features such as seed size and shape, leafiness of inflorescence, presence or absence of bipartite basal lobes on the leaves, and upright vs. spreading plants are variable within populations. As a result, it is not possible to place most individuals into one of the previously recognized five species.

Plants belonging to this complex can be distinguished morphologically by the fact that they have triangular leaves with basal lobes, and seeds with attached pericarps that have reticulately roughened surfaces. Although this may not appear to be many characters on which to recognize a species, no other taxon in *Chenopodium* possesses these features. In this genus, where species are notoriously difficult to delimit morphologically, these plants are relatively well circumscribed.

Flavonoid chemistry is a unifying feature of the *C. neomexicanum* complex. That the type specimens of all described species appear to be the same chemically is of particular interest. Also, no intra- or interpopulational chemical variation was encountered in those plants examined.

These data assume greater importance when it is considered that this chromatographic profile, so far as is known, is unique in the genus.

The leaf epidermal pattern found in this complex also appears to be a unifying feature. Due to small sampling, I cannot say that similar patterns are not found in other taxa. It is of interest to note, however, that the pattern does differ strikingly from that found in *C. fremontii* (fig. 5C), even though I have found it impossible to distinguish leaves of the two on the basis of external morphology. Preliminary studies indicate that epidermal patterns will be useful taxonomically in North American *Chenopodium* (Crawford, 1972).

When all data are considered, it seems best to recognize the *C. neomexicanum* group as consisting of a single species, namely *C. neomexicanum*. Even after the five formerly recognized species have been "lumped", the resulting taxon is much more uniform and tightly circumscribed morphologically than many others in *Chenopodium*.

The information at hand demonstrates quite conclusively that *C. neomexicanum* is distinct from *C. berlandieri*. Features of the leaves (fig. 3) and fruits and sepals (fig. 4) serve to separate the two species morphologically in all instances. Chromosomally, *C. neomexicanum* is diploid, whereas *C. berlandieri* is tetraploid. The flavonoid chemistry of the two is likewise quite distinct. Leaf epidermal patterns also are diagnostic features for separating the two species (fig. 5A,B). Although the patterns are basically similar, the difference in guard cell size is consistent.

I shall comment only briefly on the placement by Aellen and Just (1943) of *C. neomexicanum* under *C. watsonii* forma *glabrescens* (now *C. glabrescens* (Aellen) Wahl). There appears to be no justification for such a transfer, and I am in complete agreement with Wahl (1952-53) that this should not have been done. *Chenopodium glabrescens* may be distinguished on the basis of its fruits, which have conspicuously whitened, attached pericarps. In addition, the sepals enclose the fruits tightly, even in the most mature condition. There are differences between *C. glabrescens* and *C. neomexicanum* in both leaf morphology and leaf flavonoid chemistry (Crawford, unpublished).

Various features of *C. neomexicanum* raise interesting questions concerning its relationships within *Chenopodium*. Morphologically, the plants have triangular leaves that are essentially identical to those of *C. fremontii*. The seeds of *C. fremontii*, however, differ markedly from those of *C. neomexicanum* in that the pericarp of the former is smooth and easily separable. The seeds of the latter taxon are similar to those of *C. berlandieri* although, as mentioned above, they can be distinguished. Past workers have debated whether the leaves or seeds should be given greater weight in considering relationships. Standley (1916) placed the *C. neomexicanum* complex together with *C. fremontii* in his "group" Fremontiana, the unifying feature being the triangular leaves. Aellen (1929) suggested that those plants with "honey combed-pitted" seeds (as found in *C. neomexicanum* and *C. berlandieri*) should be grouped

together, but he also believed that it was more a matter of personal preference whether one chooses to use leaves or seeds as the basic criterion for taxonomic arrangements.

Chenopodium neomexicanum appears to be more closely related to *C. berlandieri* than it is to *C. fremontii*. Gross leaf morphology is the only feature that *C. neomexicanum* and *C. fremontii* share. The two differ in leaf epidermal patterns (fig. 5A,C). In addition, the flavonoid chemistry of the taxa is quite different. *Chenopodium fremontii* produces a series of kaempferol and/or isorhamnetin glycosides in addition to several quercetin glycosides (Crawford, 1972, and unpublished). It has already been mentioned that the seeds of the two species are very different. It would appear that even though the similarities between the leaves of the two are quite striking and evident, it gives a rather misleading impression of overall genetic relationships.

Based on the totality of characters, *C. neomexicanum* appears to be rather closely related to *C. berlandieri*. Although the two clearly represent distinct species, the following basic similarities should be noted: 1) the seeds of both have attached, reticulate pericarps; 2) the flavonoid chemistry of the two is similar in that they produce only quercetin glycosides; and, 3) the leaf epidermal patterns, while distinct on the basis of cell size, are quite similar.

The fact that *C. neomexicanum* is diploid and *C. berlandieri* is tetraploid is of evolutionary interest. The former taxon is the most *berlandieri*-like diploid chenopod that I have encountered. This at least suggests the possibility that plants similar to *C. neomexicanum* may be ancestral to *C. berlandieri*. Wahl (1952-53) indicated that *C. berlandieri* may have originated in the southwestern United States with speciation occurring in arid or montane areas. This hypothesis for the locality of the origin of *C. berlandieri* is near the present distribution of *C. neomexicanum*.

TAXONOMY

CHENOPODIUM NEOMEXICANUM Standley, North Amer. Flora 21:19. 1916. TYPE: USA: New Mexico, Sierra Co.: along Mineral Creek, 2250 m, 26 Sep 1904, *O. B. Metcalfe* 1413. Holotype: US!

Chenopodium palmeri Standley, North Amer. Flora 21:19. 1916. TYPE: Mexico: Chihuahua: Hacienda San Miguel, 1885, *E. Palmer* 9. Holotype: US!

Chenopodium arizonicum Standley, North Amer. Flora 21:19. 1916. TYPE: USA: Arizona: Santa Rita Forest Reserve, 1903, *D. Griffiths* 5982. Holotype: US!

Chenopodium parryi Standley, North Amer. Flor 21:21. 1916. TYPE: Mexico: San Luis Potosi: region of Cd. San Luis Potosi, 1878. *C. Parry* & *E. Palmer* 780. Holotype: US!

Chenopodium lenticulare Aellen, Feddes Report. Spec. Nov. Regni Veg. 26:152. 1929. TYPE: USA: Texas: Austin, 1918, *M. S. Young* 708. Holotype: US!

A list of specimens examined is available from the author upon request.

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ECOLOGY OF THE SAGUARO (CARNEGIEA GIGANTEA): PHENOLOGY AND ESTABLISHMENT IN MARGINAL POPULATIONS

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The saguaro, *Carnegiea gigantea* (Engelm.) Britt. & Rose (Cactaceae), has been at the center of much scientific interest since Shreve (1910) reported its failure to reproduce in some localities. Additional observations that supported Shreve's conclusion (Gill, 1942; Gill and Lightle, 1946; Hastings, 1961; Alcorn and May, 1962; Niering et al., 1963; Alcorn, 1966) led to a number of studies aimed at defining the cause of the saguaro's decline (Shreve, 1911; Lightle et al., 1942; Alcorn and Kurtz, 1959; McGregor et al., 1962; Hastings and Turner, 1965;

Turner et al., 1966; Steenbergh and Lowe, 1969; Turner et al., 1969). Since saguaro population declines had been noted in many different environments, climate was suggested as affecting either germination or seedling survival, or both. It was the aim of this study to investigate the interaction of climate and saguaro survival in marginal populations and in so doing to identify the factors limiting the saguaro's geographical distribution.

STUDY SITES

Available data suggest that the most significant climatic factors affecting saguaro germination and establishment (seedling survival) are temperature and moisture. Since it is these climatic factors that apparently limit marginal saguaro populations in the North (temperature) and in the West (moisture), investigations in these areas may provide insight as to which of these climatic factors is more important in influencing saguaro germination and survival and/or limiting extension of the saguaro's range. Consequently a study site was established in each of two marginal populations. An additional study site, located more centrally within the range of the saguaro, was also established to provide a basis of comparison.

Site 1, the "control", is at the junction of U.S. Highway 93 and the Santa Maria River (Yavapai Co.) about 68 km north of Wickenburg, Arizona. This site, with an elevation of 1136 meters, was judged to be generally representative of saguaro populations (about 50 per hectare). Other dominant perennials occurring with the saguaro are *Cercidium microphyllum*, *Larrea divaricata*, *Acacia greggii*, and *Prosopis juliflora* (listed in order of abundance).

Site 2 is in the southern portion of the Hualapai Mountains (Mohave Co.) on Alamo Road 45 km southwest of Yucca, Arizona at an elevation of 595 meters. This area supports one of the northernmost populations of saguaros with the majority (about 37 per hectare) found on south-facing slopes. The study area supports the greatest numbers of species of both succulents and non-succulents of the sites investigated. Notable species present, in order of abundance, are *Opuntia bigelovii*, *Ambrosia dumosa*, *Opuntia acanthocarpa*, *Cercidium microphyllum*, *Larrea divaricata*, *Hymenoclea salsola*, *Fouquieria splendens*, and *Yucca brevifolia*.

Study Site 3 is in the Whipple Mountains (San Bernardino Co.) near the eastern border of California and runs along the Metropolitan Water District's access road west of Parker Dam. This site supports the most substantial population of saguaros found in California (ca 120 individuals) and is located on the western border of the saguaro's geographical range. Because of low saguaro density the study site is very large (about ten square km) and the elevation ranges from 107 to 366 meters. The density of saguaros is about four per hectare in the eastern part of the study site, where plants are limited to north-facing slopes; however, near the junction of Copper Basin Reservoir access road a very substan-

tial stand of saguaros (about 12 per hectare) occupies all the slopes of a circular range of peaks, with the greatest density on the southeast-facing slopes. The percent ground cover and densities of all species were lowest in this study area when compared with Sites 1 and 2. Dominant perennials in this area, other than the saguaro, are *Larrea divaricata*, *Hymenoclea salsola*, *Opuntia bigelovii*, and *Encelia farinosa* (in order of abundance). *Cercidium microphyllum*, also a dominant, occurs predominantly in the washes.

MATERIALS AND METHODS

Shreve (1910) and later Hastings and Alcorn (1961) measured the rate of growth of selected individuals of the saguaro and determined a relationship between height and age. This relationship was used in the present study to estimate age and germination dates of sampled individuals. On the basis of the number of individuals surviving within each height class (set at 61 cm intervals), saguaro establishment (i.e., germination and seedling survival) was compared in the three study areas. Then by correlating saguaro establishment periods (i.e., the number of saguaros that germinated and survived to present during the time interval corresponding to the 61 cm height increment) with available weather records, climatological requirements for establishment in each study area were estimated.

Saguaro heights were determined on two different dates at each study site. Data were first collected on December 28, 1971, for Sites 1 and 2, and on January 12, 1972, for Site 3. Individual heights were estimated with the use of a fixed 6-foot standard placed beside the cactus. Heights of additional individuals were determined on April 28 and 29, 1972, using a graduated telescoping aluminum pole, capable of expanding to 7.5 m. Selection of individuals for height measurements was by random selection of a sampling area within the study site and then quota sampling within that area.

Because shade, which may be provided by closely associated plants ("nurse-plant") or rocks ("nurse-rocks"), has been shown to be a basic requirement for seedling survival (Turner et al., 1966), the species of "nurse-plant" or the indication of a "nurse-rock", if present, was noted at the time of height determination. In a few cases where only "nurse-plant" remains were found, no attempt was made at the plant's identification, but the association was recorded. Vigor of the saguaros sampled was estimated on a scale of 0 (dead) to 3 (healthy).

To provide phenological comparison between study sites, reproductive activity was recorded. Selected individuals were tagged and the numbers of flower buds and open flowers were counted. Twenty-five saguaros were sampled in each study area on April 28 and 29, 1972, and on May 27 and 28, 1972, the numbers of flowers maturing into fruit on these individuals were recorded. The selection of individuals was also done by random selection of a sampling area within the study site and by quota sampling of adjacent individuals of reproductive age.

RESULTS AND DISCUSSION

Height class frequencies for the three study sites are shown in Figure 1. Comparison of the means of the estimated heights and of the measured heights for each sample showed agreement at the 95 percent confidence level; therefore all height determination data are included in the figure and calculations. A close similarity between Sites 1 and 2 is most notable when comparing height classes and establishment patterns. Approximately 37 percent of the individuals sampled became established in both Sites 1 and 2 between 1916 and 1936, with maximum establishment during the period 1924–1930 (13 percent and 14 percent respectively). However, in Site 3 only 5 percent of the individuals sampled had become established between 1924–1930 and a total of only 17 percent between 1916 and 1936. The Site 3 establishment pattern also differs during the period 1908–1915 when 20 percent of the sampled individuals became established; Sites 1 and 2 show only 4 percent and 3 percent, respectively. The close similarity of establishment patterns of Sites 1 and 2, and the more or less opposite relationship for Site 3 could suggest error in applying growth rate data from saguaros that were measured in the Saguaro National Monument (i.e., by Hastings and Alcorn, 1961) to those individuals found near Parker Dam (Site 3). Or, this relationship may suggest that conditions for germination and establishment are very different during the same periods of time in areas near Site 3 than those near Site 1 and Site 2. But, similar establishment periods can also be noted for all three study sites (1900–1907, 1916–1923, 1927–1940). With both contrasting and similar establishment patterns during the

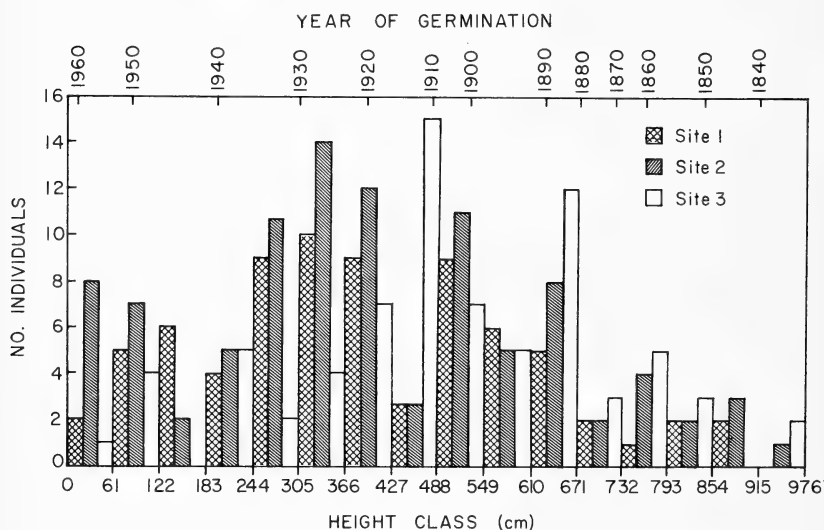


FIG. 1: Height-age distribution of saguaros in Sites 1, 2, and 3.

same periods for the three study areas it is impossible to resolve whether these establishment patterns are due to misapplication of growth rate data or to variations in germinating and survival conditions.

Shreve (1910) and later Hastings (1961) presented similar height and frequency studies for populations sampled in areas near Phoenix and Tucson, Arizona. They described how the slope of the height vs. frequency curve for a population gives an indication of the dynamic state of that population (i.e., whether it is increasing, stable, or declining). Applying this analysis to the populations included in this study, all study sites suggest declining populations. An exception may be Site 2, which indicates recent (1940–present) high establishment and low mortality (3 percent).

The majority of individuals in each study site were included in the healthiest vigor category (81 percent in Site 1, 89 percent in Site 2, 78 percent in Site 3) suggesting that most of the individuals have the capacity to reproduce (ability to produce flowers, fruits, and seeds). However, the phenological data presented in Table 1 indicate that a very low percentage of individuals actually did reproduce in 1972. At best only 32 percent (Site 1) of the individuals of reproductive age were observed in flower in 1972 and this percentage is below what would be found near Tucson, Arizona (R. Hastings, personal communication). In addition to the percentage of individuals in flower, the height and the range of height of flowering individuals also varied between study sites. The range of heights (and therefore age) of flowering plants was similar for Sites 1 and 2; however, in Site 3 no individuals less than 488 cm (60 years) were found in flower. Alcorn (1961) stated that saguaros begin to flower between the ages of 40 and 50 years (300 cm to 370 cm tall), and the individuals sampled in Sites 1 and 2 substantiate this.

Flowering individuals in Site 1 appeared to be uniformly distributed but in both Sites 2 and 3 there were distinct locations where flowering occurred. In Site 2 flowering individuals occurred only in washes and on higher slopes, and in Site 3 all the individuals found with flower buds

TABLE 1: SUMMARY OF REPRODUCTIVE ACTIVITY OF TAGGED SAGUAROS

Parameter	SITE 1	SITE 2	SITE 3
Individuals with flower buds	32%	24%	8%
Range of heights (cm) of individuals with flower buds (Ave.)	335–793 (655)	366–823 (710)	488–640 (723)
Fruit set based on the percent of flowers	90%*	85%*	10%

* Flowers buds still maturing on date of sampling.

were located in washes. These location criteria and the indication that Site 3 is the most arid of the three sites (figs. 2, 3, and 4) suggest that flowering is influenced by moisture.

The percent of flowers developing into fruit was highest for Site 1 (90 percent), but the percent of flowers in various stages of fruit maturation in Site 3 was considerably lower (10 percent). Although nighttime pollinator analysis was not included in this study, the abundance of daytime pollinators (hummingbirds, bees, wasps, and beetles) and the fact that at least a low percent of flowers matured into fruits suggest that the poor fruit set is not the result of a lack of pollinators here—even though those noted are not the saguaro's most commonly identified pollinating agents (McGregor et al., 1959, 1962; Alcorn et al., 1959, 1961). Based on the number of individuals with flower buds and the percentage of fruit set, the establishment potential is less in the two marginal populations of saguaros than that found in the more central population. Declines in these populations may then be partially explained on the basis of low reproductive potential. However, because of the critical effects of temperature and moisture on seed germination and seedling survival (Kurtz, 1960), climatological influences on saguaro establishment must also play an important role in an explanation for population declines.

After germination an important factor for seedling survival is the amount of summer (July and August) precipitation, for it is during this time that the saguaro is most efficient in taking up water (Hastings, 1961). An additional barrier to seedling survival is the intensity of the dry, hot periods (May and June) preceding summer rainfall (Turner et

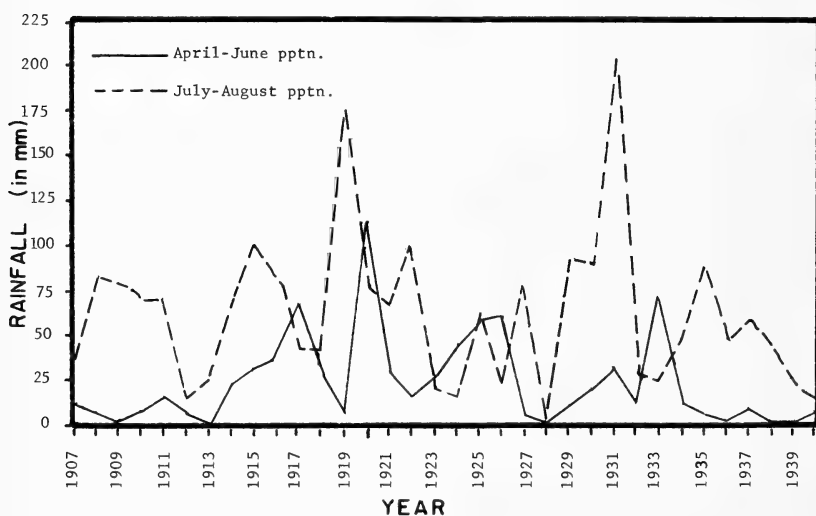


FIG. 2: Rainfall 1907 - 1940 for Site 1.

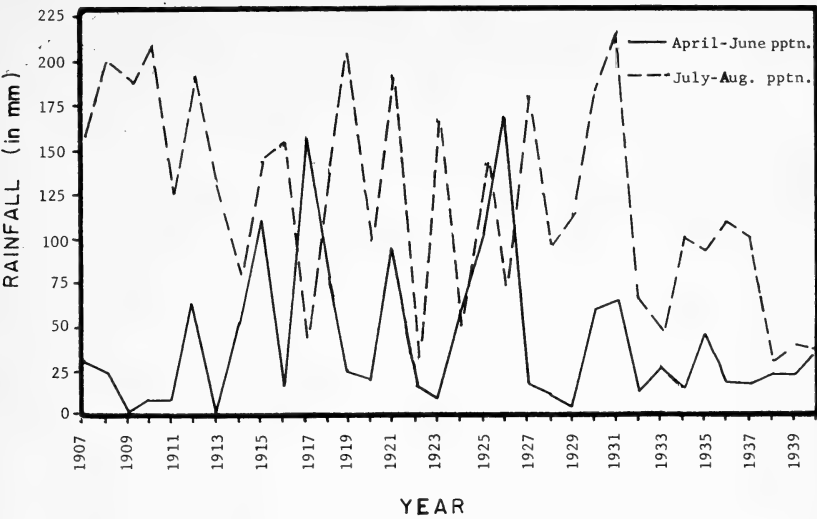


FIG. 3: Rainfall 1907 – 1940 for Site 2.

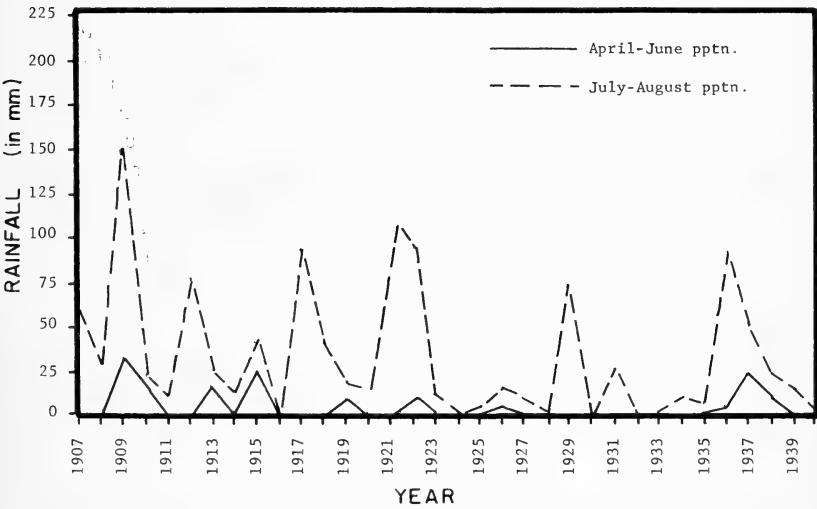


FIG. 4: Rainfall 1907 – 1940 for Site 3.

al., 1966). Climatic data from nearby weather stations (U.S. Weather Bureau, Climatic Summary of the U.S., 1893–1930, 1931–1952, 1951–1960; U.S. Weather Bureau, Climatological Data: Arizona, 1961–1965; U.S. Department of Commerce, Climatic Summary of the U.S. Suppl. for 1951–1960; U.S. Department of Commerce, Climatological Data: Arizona 1961–1965, 1966–1970; Headgate Rock Dam Weather Station

Records, 1953–1967) show that for Site 1 during the period 1907–1940 April–June and July–August precipitation correlates very closely with the number of saguaros established (fig. 2). The correlation supports the contention that there are particular precipitation requirements for both these periods and further suggests that without some minimal amount of precipitation during April, May, and June, regardless of the amount received during July and August, there would be very little or no establishment of saguaros. However, when April–June precipitation is sufficient to prevent dehydration of saguaro seedlings, the degree of establishment is proportional to the amount of precipitation received during the period from April to August. Thus the greatest establishment occurred when a year of high July–August precipitation was followed by a year with high April–June precipitation (e.g., 1916–1917 and 1925–1926, fig. 2). Precipitation data for the same period (1907–1940) are presented in Figure 3 for Site 2 and support this contention. The April–June precipitation requirement is more apparent for Site 2 for the figure shows significant establishment during a period of increasing April–June precipitation (1920–1926), which would allow for the survival of seedlings germinated over the entire six years. However, other factors (rodent populations, for instance) are also influenced by temperature and precipitation and may also be important to the observed patterns. The April–June precipitation requirement is not as definitive for Site 3, although the amount of July–August precipitation is again related to the degree of establishment (fig. 4). Site 3 experiences temperatures on an average of 2°C higher during the winter months and consequently some winter precipitation may be available to young seedlings for restoration of lost water.

Site 3 also differs from the other two study sites in having the highest percentage of individuals (86 percent) associated with “nurse-plants”, even though potential “nurse-plant” density is the lowest (maximum of 75 plants per hectare). In Site 1 where “nurse-plant” density is high (10 times that of Site 3), 74 percent of the individuals were associated with a “nurse-plant” while in Site 2 with the highest density of potential “nurse-plants” only 10 percent of the saguaros were associated with “nurse-plants”. Although the highest percentage of saguaros associated with “nurse-rocks” (15 percent) was in Site 2, Site 3 still had the greatest number of individuals (90 percent) associated with shade producing objects. Perhaps the explanation for the establishment of individuals in Site 3 during drier May–June periods is related to the protection offered by the shade of either “nurse-plants” or “nurse-rocks”. Lowe and Hinds (1971) showed that radiation temperature is up to 25°C higher in the open than under a paloverde (*Cercidium* sp.) Thus a saguaro seedling growing under a paloverde might be subjected to less dehydration stress during the May and June hot, dry period than a seedling growing out in the open. All of the individuals with “nurse-plants” in Site 3 were associated with paloverdes and not with other, perhaps less protective, “nurse-

plants" found in the other study areas. Further analysis at Site 3 showed that individuals without a "nurse-plant" fell into distinct height categories (i.e., at 183 cm four out of five individuals were not associated with a "nurse-plant") and that the corresponding germination dates show the April-June period to be considerably wetter (four times) than periods when only saguaros with "nurse-plants" survived.

CONCLUSION

Data included in this study clearly support Shreve's conclusion that in many environments saguaro reproduction does not meet replacement requirements necessary to maintain stable populations. One explanation for the population declines may be low reproductive potentials such as those found for 1972 in each study site included in this investigation.

The climatic criteria for germination and establishment have been shown to be strict enough that only exceptional years of high summer and spring rainfall result in significant saguaro establishment. In addition, with climatic trends in opposition to establishment criteria for the saguaro, declines in some marginal populations (as indicated in this study) are to be expected. Populations in the more northern portions of the saguaro's range may however, increase in size and number in future years because of the general climatic trend of increasing temperatures. For the western boundary range expansion does not seem likely, for weather data indicate that the saguaro establishment requirements are only rarely met in California deserts. Indeed, population declines and range reduction in California are more likely to occur in the future.

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CALIFORNIA SPECIES OF CORDYCEPS PARASITIC UPON ELAPHOMYCES

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During the past several years *Cordyceps capitata*, a pyrenomycetous parasite of *Elaphomyces*, has been found in the coastal forest of California from Sonoma County northward to Del Norte County and often abundantly so in Mendocino and Humboldt counties. Recently one of

us (Largent) made a collection of *Cordyceps ophioglossoides*, a similar type of parasite, in Del Norte County near the Oregon border. All collections have been made in areas where there was a deep layer of organic matter, and they were always found in dense mixed forests. No collections have been made by us from any other part of the state.

As far as can be determined there are no reports in the literature of the presence of any species of *Cordyceps* parasitic upon *Elaphomyces* from California. Apparently the first and only report of the presence in the state of any of these fungi is that by Harkness and Moore (1880) in which they reported *Torrubia (Cordyceps) militaris*, a species parasitic upon insects, from the vicinity of Sausalito in Marin County. Seaver in his treatment of the genus in 1911 failed to report any species from the West Coast. Mains (1957) in a more recent monograph of North American species reported both *C. capitata* and *C. ophioglossoides* from Oregon and Washington. This present report extends the range of these two species into northern and central California.

Since there are no published descriptions of California material, short descriptions of both species are included. Color citations for *C. capitata* are from Ridgway (1912) while those for *C. ophioglossoides* are from Kornerup and Wanscher (1961).

Key to the species of *Cordyceps* parasitizing *Elaphomyces*

- Stromata clavate; ascigerous portion not strongly differentiated from stipe *C. ophioglossoides*
Stromata capitate; ascigerous portion globose, conic, ovoid or cylindric, abruptly and clearly differentiated from the the stipe *C. capitata*

1. *Cordyceps ophioglossoides* (Fries) Link, Handbuch 3:347. 1833.

Stromata one-third to one-fourth the length of the stipe, not sharply differentiated from the stipe, 13–25 mm long, 2–8 mm thick, clavate, often flattened, even spatulate and grooved at the apex, light olive-brown to dark olive-brown to almost black (3–4, D, 7–8, to 3–4, E, 7–8), tuberculate due to protruding perithecial ostioles; cortex fibrous, concolorous with the stipe base and rhizomorphs (3–4, A–B, 7–8).

Perithecia ovoid with a short neck, 240–600 μ wide, embedded within the stroma; asci cylindrical, 8-spored, unitunicate, narrowing below, 122–306 by 6–7 μ , apex swollen, 6–10 μ wide, with two large, non-amyloid elliptical areas within that do not stain with 3% KOH, phloxine, or Congo Red; ascospores scolecosporous, colorless, 110–250 by 1.5–2.0 μ , breaking up into one-celled segments, 2.5–5.0 by 1.5–2.0 μ ; paraphyses entangled but free, filiform, slightly clavate at the apex, colorless.

Stipe 18–49 mm long, 2–6 mm wide at the apex, up to 10 mm wide on entering *Elaphomyces*, yellowish to yellowish orange (3–4, A–B, 7–8) at the basal one-third to one-half, olive-yellow to light olive-brown (3–4, D, 7–8) at the apical two-thirds to one-half, terete, often flattened, frequently longitudinally grooved.

Collections studied: *Largent* 4145, 5217 (HSC). Extremely abundant, covering nearly 20 square meters, beneath Tanbark oak trees, at the very end of Winchuck Road along the South Fork of the Winchuck River, Six Rivers National Forest, northern Del Norte County, California, 23 Oct 1971.

2. *Cordyceps capitata* (Fries) Link, Handbuch 3:347. 1833.

Stromata 5–20 mm high, 5–20 mm broad at widest portion, conic to convex to subcylindric to subglobose, not clavate, abruptly and well differentiated from the stipe, surface dry, more or less uneven, punctate-roughened from the ostioles of the perithecia, colored dark reddish brown to dark olive-brown, “mummy brown” to “warm sepia” to “bister” to sometimes as pale as “verona brown”, composed of a cortical layer containing numerous perithecia, hyphae pseudo-parenchymatous, no distinct ectal layer; context white, loosely interwoven.

Perithecia ovoid to flask-shaped 650–825 by 260–430 μ , embedded in the cortical layer, walls well differentiated and colored pale brown to tan; asci hyaline, long and narrow, 400–545 by 8–11 μ , with a thickened ring at the apex; ascospores scolecosporous, hyaline, non-amyloid, usually breaking up into one-celled segments that are 15–27 by 1.5–2.5 μ ; paraphyses hyaline, unbranched, tangled.

Stipe 30–80 mm long, 5–15 mm broad at apex; equal or occasionally flattened, usually crooked or bent in one or more places; surface dry, conspicuously fibrillose to fibrillose-scaly; outer layer sometimes becoming broken or rimose with some of the fragments becoming recurved, colored yellow, “primuline yellow” to “yellow ocher” to “antimony yellow” to near “wax yellow”, pallid to whitish at the base, no gray or olive colors noted, context white, floccose; base attached to ascocarps of *Elaphomyces*.

Scattered to gregarious to sometimes abundant in soil in mixed forests in coastal areas of northern California.

Collections studied: Humboldt Co.: *Theirs* 14502, 18380, 24344, 24346. Mendocino Co.: *Largent* 104; *Peters* 729; *Thiers* 8921, 9430, 9600, 9724, 9843, 10052, 10729, 11032, 14638. Sonoma Co.: *Largent* 5544, 5701; *Thiers* 30718. All collections deposited in the cryptogamic herbaria of either California State University—San Francisco or California State University—Humboldt.

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WALLACE ROY ERNST, 1928–1971

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It is difficult to write about a close friend of long duration. The better one knows an individual, the harder it is to write the things one wants to say, and at the same time to write what the friend would want to have written about him.

What we write is in three parts. The first is by Stanwyn Shetler and is the tribute he wrote to Wallace Roy Ernst and read before the 18th Annual Systematics Symposium at the Missouri Botanical Garden on October 16, 1971. The second part is by John Thomas. The third part (by both of us) is an account of some of the important events and dates in Wally's life and a list of his writings.

— 1 —

Although Wally would be uncomfortable if he were here today to hear us, it is altogether fitting that we should pause a moment at this Symposium, which he frequently attended, to pay tribute to his memory. I am honored to be asked to say a few words about our late colleague and friend.

Wallace Roy Ernst died peacefully Friday night a week ago, the 8th of October, at the Washington Hospital Center, Washington, D.C., after a long and often painful illness with cancer. He was only 43 years of age. Just a year ago Wally was still pursuing his research with full vigor, although signs of ill health had been building up. Through the late fall and early winter [of 1970] his health deteriorated rapidly, and in late January of this year Wally learned the fateful news that he was dying of cancer. Wally accepted this news stoically and began an heroic but foredoomed fight to stay on his feet and continue his work. Against considerable odds he did continue his research between periods of hospitalization and completed his 5-year effort on the genus *Lamourouxia* (Scrophulariaceae), sending it to the Smithsonian Press in the summer. This paper is now in galley proof. For Wally, this cleaned the slate and brought him great satisfaction. Even so, he was not content to brood on his fate and wait idly for death, and he began to lay plans for work on

the Theophrastaceae. But for this will and fierce determination, Wally would have succumbed months earlier. During all the long months of illness, at times marked by excruciating pain, I never once heard him complain. Instead he would ask about the well-being of his many friends who came to see him. He was touched and constantly amazed by the number of friends throughout the world who took time to remember him with cards, letters, flowers, gifts, and personal visits.

I first learned to know Wally when he came to work at the Smithsonian in 1963. Immediately, we became fast friends. Wally was a faithful friend who lived without pretention and expected as much of his friends. He abhorred artificiality and officiousness and sometimes was misunderstood for this. I will always remember him as a person who said and stood for what he believed.

In his professional work, Wally set and demanded high standards, no less of himself than of others, and he would not compromise his standards even though they sometimes brought him frustrations. During his short years, however, he found time to conduct studies in a broad range of groups—Papaveraceae, Fumariaceae, Capparidaceae, Loasaceae, Scrophulariaceae, and others. He had an extremely broad knowledge of plant families and often put this knowledge to use in helping his colleagues or the lay public with their identification problems.

Wally's summers with the National Park Service during his earlier years imbued him with a lasting concern for the quality of public education in natural history.

He was a refined and cultured man, who enjoyed art, music, and fine cuisine. He loved to collect pottery, paintings, and Navajo rugs.

Wally loved his native state of California and always gave his California friends and memories a special place in his heart and mind. He taught me the delicate pleasures of its vineyards and the exquisite beauties of its landscapes and natural history. One of the most touching moments I witnessed during his illness came when he showed me Roxana Ferris' latest book on California wildflowers, *Flowers of the Point Reyes National Seashore*, which she so thoughtfully had sent him. The memories it brought back caused his eyes to sparkle with warmth and feeling. His ashes are being returned to his beloved land.

Wally was genuine. A good and decent person, a kind and gentle friend, an honest and worthy colleague. He deserved his full three-score and ten years. He will be missed, and we shall always remember him.

— 2 —

I first met Wally in the very late fall of 1952. He was a graduate student with Harlan Lewis at the University of California at Los Angeles. I was just out of the U.S. Navy and he was about to be in the U.S. Army. Our paths did not cross again until Wally came to Stanford in the fall of 1955 to begin his work for a doctorate.

Wally worked very hard to attain his degrees. This he did largely on

his own financial base and often by the use of frugal measures. Perhaps it should not be mentioned, but he sometimes slept on the roof of the old botany building at UCLA to avoid having to pay for the gasoline to drive to his parents' home in the Highland Park District of Los Angeles, some 16 miles away. I think that much of Wally's extreme generosity stemmed from his early experience of having to make so much out of limited financial resources.

At Stanford as graduate students we became friends, shared neighboring desks, and exchanged many of our thoughts, fears, and delights.

Wally was an expert gardener. And most amazingly, he did his gardens without the expenditure of much money. What made his garden grow was his green thumb, genuine expertise, good design, and the physical effort he put into it. His Stanford garden was near perfect, because Wally was a perfectionist.

Wally's dissertation with Richard W. Holm was a comparative study of the Papaveraceae. The main emphasis was on floral morphology and this continued to be one of his main interests. During his graduate work he participated in much more departmental teaching than the current crop of graduate students have become accustomed to expect. He assisted not only in botany courses, but also in several courses in general biology and zoology. In all he was very good—Wally was one of those people who just plain knew a lot about living things.

At earlier times in his career, and as a student at Stanford, he served as a ranger naturalist in the National Park Service, particularly in the Kings-Sequoia area of the Sierra Nevada of California and at Crater Lake in the Oregon Cascades.

Wally, like all of us, could be diffident and difficult. On the day he took his final examination for the doctorate, he would not call to let anyone know that he had passed, much less allow any kind of a celebration. I had to call him, after finding out that he had done exceedingly well, to congratulate him. Wally was always very modest about his own accomplishments and tended to deprecate them.

From Stanford Wally went to a temporary position at the Herbarium of the University of California at Berkeley. Here he put new life into the California Botanical Society. Due to his efforts, attendance doubled almost overnight at the monthly meetings. After some nine months at Berkeley, he went to Cambridge, Massachusetts, to work in the Gray-Arnold complex at Harvard University on the *Generic Flora of the Southeastern United States*. It was during this period that he put the final touch of perfection on his dissertation.

After contributing a number of treatments to the Southeastern Flora, Wally was appointed to the staff of the Department of Botany in the National Museum of Natural History of the Smithsonian Institution in Washington, D.C. His initial assignment was to aid in the work on certain floras of the southwestern part of the Pacific and his official responsibility in the United States National Herbarium was the flora of Eurasia.

During Wally's tenure at the Smithsonian, I had a number of occasions to visit him. He was always most generous, insisting to a fault, for instance, that I stay with him, even though this meant that he would sleep on the floor while I slept comfortably in the bed he had vacated. Wally's generosity was one of his hallmarks. On more than one occasion, I deplaned in Virginia or Maryland in the very early morning, and there was Wally despite my positive assertions that I could get into the center of the District of Columbia by way of public transportation. In his time at the Smithsonian, Wally met and took to the airport more visiting botanists than one can count. And many of these he entertained either in his small efficiency apartment, or in Washington's interesting and better restaurants or both!

Not all of Wally's Smithsonian experience was peaches and cream for him personally. When he first arrived, his space was a desk in an alcove in the "Castle". His principles of excellence, of perfection, and his insight into the nature and philosophy of systematic biology, brought him into conflict with some of his colleagues. Wally would do anything to help if there was a scientific rationale involved. If someone or something seemed stupid to him, he was adamant to the point of being obstinate. He was in this way more openly honest than most of us are. Fortunately he lived to see his principles vindicated and his early problems surmounted, as he was for several years before his death a full curator in the Department of Botany.

During all of Wally's graduate and scientific career, the one person he held in greatest esteem was Henry J. Thompson. Not only was Harry involved in his graduate work at UCLA, but he continued as a friend and collaborator. Both Harry and Wally won the Cooley Award of the American Society of Plant Taxonomists individually. They won it jointly later on.

Wally's Washington years were relatively happy ones. He did miss a garden and the easy access to the poppies of the West. This was offset to an extent by the opportunities to visit the Caribbean, particularly the island of Dominica, many parts of Europe, Russia, and North Africa. An additional satisfaction was his appointment as Professor in absentia at the University of Kansas, an appointment that carried a small, but nevertheless substantial, stipend.

The first inkling I had of Wally's illness was in December of 1970. He called early one morning from Los Angeles, where he was visiting his mother, to say that he had to get back to Washington for his work was very pressing. This did seem peculiar in retrospect. Early in January of 1971 he found that he had cancer. I quote from his letter of February 1, 1971:

"For a little more than two weeks I have been at the Washington Hospital Center. . . . The prognosis is very grim. Soon will start some chemical therapy which may—or most likely will require surgery to place

a catheter in the hepatic artery. With luck I will be able to go to my apartment, work a little, and have outpatient treatment. Slowly I am being able to face what this means and today I am feeling a lot better. My Mother only knows that I am sick and will receive additional treatment. I really don't want everybody to know about this but a liver tumor is a liver tumor. I have had the best of everything, fine doctors, and a wonderful friend who helps me."

Wally knew that he would die, but even then, as always, he did not complain for himself. I saw him last in May of 1971. He still insisted upon being the perfect host, even though it pained him much.

During his illness Wally was taken care of with kindness and consideration by Mark Carnivale, a friend of many years. Mark provided the comfort and help Wally needed as he became progressively more incapacitated. Wally died on October 8, 1971. His wish was that his ashes be scattered over the southern Sierra Nevada of California, an area where the poppies he studied and loved occur by the millions.

The irony of it all is that when we were students, we used to joke that: "Only the good die young." Wally was very, very good.

— 3 —

Wally was born in Los Angeles, California, on May 2, 1928. His father was Charles Joseph Ernst, 1893–1957, who came to Los Angeles from Kansas. He worked for the City of Los Angeles throughout most of his career. Wally's mother is Velma B. Ernst, a native of Southern California, and lives in Los Angeles. Wally had only one sibling, a brother, Charles Edwin Ernst, who for many years was involved in county management, particularly in San Mateo and Los Angeles counties.

Wally attended elementary and high schools in Los Angeles and graduated from Franklin High School in 1946. From 1946 to 1948 he attended Los Angeles City College and received an A.A. degree in life sciences in 1948. From there he went to the University of California at Los Angeles, receiving his A.B. degree in botany in 1950 and his M.A. degree in plant sciences in 1953. He was in residence at Stanford University from 1955 through 1960, and he received his Ph.D. in biological sciences in June of 1962.

From Sept. 21, 1953, through Sept. 2, 1955, Wally served in the United States Army in the capacity of a medical laboratory technician. His service included a period of time in Germany.

For several summers, starting in 1949, he worked in a number of the western National Parks, mainly Yosemite, Kings, Sequoia, and Crater Lake, in capacities that ranged from lifeguard to labor crew foreman in blister rust control to ranger-naturalist.

Wally's botanical field experience included all the western and southwestern states, with particular emphasis on the Pacific States, Baja California and many other parts of Mexico, Dominica and other islands in

the Caribbean, New England, North Africa, and Europe including European Russia.

A notice of Wally's death appeared in Madroño 21:69, 1971. *The Washington Post* of Tuesday, October 12, 1971, and the *Evening Star* (Washington, D.C.) of the same date carried short obituaries. *The Smithsonian Torch* in the Fall 1971 number carried a short notice. Volume 21 of Madroño was dedicated to Wally and his picture constitutes the frontispiece of that volume.

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The Loasaceae in the southeastern United States. J. Arnold Arbor. 44:138-142. (With H. J. Thompson)
The genera of Hamamelidaceae and Platanaceae in the southwestern United States. J. Arnold Arbor. 44:193-210.
Contrasting patterns of variation in *Eucnide* and *Sympetaleia* (Loasaceae). Amer. J. Bot. 50:638. (With H. J. Thompson, abstract)
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Review of: Index to European taxonomic literature for 1965, compiled by R. K. Brummitt. Madroño 19:58-59.

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Two new species of *Lamourouxia* (Scrophulariaceae) in Mexico. *Madroño* 20:342-346. (With M. F. Baad)
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1971. Review of: *Flora of the Galapagos Islands*, by I. L. Wiggins and D. M. Porter. *Madroño* 21:111-112.
1972. Floral morphology and systematics of *Lamourouxia* (Scrophulariaceae: Rhi-nanthoideae). *Smithsonian Contr. Bot.* 6:1-63.

NOTES AND NEWS

EDITORSHIP OF MADROÑO.—Robert Ornduff has resigned the editorship of *Madroño*. The Board of Directors of the California Botanical Society have appointed John L. Strother and Alan R. Smith (both members of the staff of the herbarium, Department of Botany, University of California, Berkeley 94720) Editor and Associate Editor, respectively.

ANNOUNCEMENT OF MEETING.—The California Botanical Society will hold its first meeting of the fall October 20-21, 1973, at Rancho Santa Ana Botanic Garden. The meeting will take the form of a series of contributed papers, by students, in the areas of plant systematics and ecology. Members and non-members of the Society both professional and non-professional, are invited to attend. Advance registration (no fee) is requested. For registration forms or additional details contact ALAN R. SMITH, Department of Botany, University of California, Berkeley 94720, or DAVID YOUNG, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, California 91711.

TWO OREGON PLANT RECORDS.—*Lewisia Cotyledon* var. *Howellii* (Wats.) Jeps. was previously known in Oregon from Josephine and Curry Counties. On 25 March 1973, my husband and I discovered a new station in Cow Creek Canyon, Douglas County, Oregon. While climbing a large bluff of conglomerate composition we sighted one plant beginning to bloom. Upon searching, we counted 66 separate plants. Returning 15 April, we found the plants in full bloom and located many more small colonies with the aid of binoculars. They are growing in small, mostly inaccessible colonies of from one to fourteen plants at 300 to 450 meters with principally a southern exposure. We found a few plants with a western exposure and one plant on the north side of the bluff. One specimen is deposited at OSC.

Adiantum Jordanii K. Mull. has been reported from as far north as the Rogue River Canyon in Oregon. In May 1972, Mrs. Perry Thiele discovered this species at the base of a conglomerate bluff near the small town of Tenmile, Douglas County, Oregon. On 25 March, 1973, Mr. & Mrs. O. E. Fosback located additional colonies of *Adiantum Jordanii* in Cow Creek Canyon, Douglas County, Oregon in the same area as *Lewisia Cotyledon* var. *Howellii*.—MRS. O. E. (JOAN) FOSBACK, 157 W. Bodie, Roseburg, Oregon 94770.

ORNITHOSTAPHYLOS (ERICACEAE) IN CALIFORNIA.—*Ornithostaphylos* J. K. Small (N. Amer. Fl. 29:101. 1914) is a monotypic segregate of *Arctostaphylos* Adanson, with whorled bifacial linear leaves that have revolute margins and are finely whitish puberulent beneath, and with each pyrene two seeded and almost completely two celled. *Ornithostaphylos oppositifolia* (Parry) Small, known in Baja California as Palo Blanco, is a shrub or small tree commonly 2 to 5 meters tall, with a burl and with smooth-peeling whitish bark on the main branches. The leaves are predominantly three at a node, seldom opposite or subopposite and then apparently on only a few branchlets; on vigorous basal shoots they may be in fours or fives. Panicles of small long-pedicelled urceolate flowers are borne February to April and small red drupes May to August.

This shrub is common and widespread in the chaparral of northwest Baja California, in the north towards the coast and down to 100 meters elevation, southward at 500 to 1200 meters on the west slope of the Sierra San Pedro Mártir. It extends south at least to Rancho el Ciprés (near 30°23'N.) and to the slopes above Agua Amarga (near 30°28'N.). Hitherto known only from Baja California, it may now be reported from just north of the boundary near Boundary Monument 256, ca 5 km (3 miles) west of San Ysidro, San Diego County (Moran 16722, 20351, SD &c.). There it is a dense rounded shrub 1 to 1¾ meters high, occasional locally in chaparral-with-sage-scrub at about 125 meters elevation, at the northern end of the Tijuana Hills. Its most common shrubby associates are *Ceanothus verrucosus* Nutt. and *Salvia mellifera* Greene. Also present are *Yucca schidigera* Roetzl, *Eriogonum fasciculatum* Nutt., *Adenostoma fasciculatum* var. *obtusifolium* S. Wats., *Cneoridium dumosum* (Nutt.) Hook. f., *Rhus integrifolia* (Nutt.) Rothr., *R. laurina* Nutt., and *Artemisia californica* Less.

For want of space, acknowledgments are postponed to a future issue.—REID MORAN, Natural History Museum, San Diego, California 92112.

A SECOND LOCATION FOR *NOLINA INTERRATA* GENTRY (AGAVACEAE).—*Nolina interrata* has been known to occur only at the type locality behind the Dehesa School near El Cajon, San Diego County, California. We have found a second population of this species about 7 kilometers southwest of the type locality just off the Skyline Truck Trail about 1.6 kilometers east of the junction with the Lawson Valley Road (T16S, R2E, S31, 32). It is north of the road on an unnamed hill between elevations of about 670 to 700 meters (Zedler and Keeley 3476, SD).

The population is distributed over the top of the hill in an area of about 5 hectares, and consists of at least 50 distinct clumps. The presence of underground platforms bearing the aerial rosettes in all of the individuals seen, the flat leaves, and the complete absence of significant above-ground stems make it quite certain that this is *Nolina interrata*. We believe that this population is an old one because many of the platforms are a meter or more in their longest dimension, and the surrounding chaparral is relatively undisturbed, although the presence of fencing would indicate that there has been grazing in the past. The entire area occupied by the population was burned over in the Laguna Fire of 1970, but all of the *Nolina* observed re-sprouted. Many of the clumps have produced flowering stalks since the fire, but no recent reproduction was observed.

Gentry (Madroño 8:179–184, 1946) remarked that *Nolina interrata* was not “a close component of the chaparral”. This is not true at the new location where it is found in close association with chaparral shrubs such as *Rhus ovata*, *Rhus laurina*, *Adenostoma fasciculatum*, *Yucca whipplei*, *Xylococcus bicolor*, *Arctostaphylos glandulosa*, *Salvia clevelandii*, *Lotus scoparius*, *Rhamnus crocea*, *Tetracoccus dioicus*, and *Helianthemum scoparium*. The discovery of this new location to the south of the type locality suggests that Gentry's belief that *Nolina interrata* may be found in Baja California is likely to prove correct.—PAUL H. ZEDLER and JON E. KEELEY, Biology Department, California State University, San Diego 92115.

LITERATURE OF INTEREST

The taxonomic status of *Pentachaeta* and *Chaetopappa* with a revision of *Pentachaeta*. By Gene S. Van Horn. Univ. Calif. Publ. Bot. 65:1-41. 1973. Concludes that two asteraceous genera that are sometimes merged are not closely related; one new subspecies described in *Pentachaeta*.

The peristome of *Fissidens limbatus* Sullivan. By Dale M. J. Mueller. Univ. Calif. Publ. Bot. 63:1-34, 35 plates. 1973. Morphology, development, and histochemistry of the peristome in the moss *Fissidens limbatus*, using light and transmission electron microscopy.

George B. Hinton, collector of plants in southwestern Mexico. By James Hinton and J. Rzedowski. J. Arnold Arbor. 53:140-181. 1972. Includes collecting itinerary (with map) and biographical notes.

REVIEWS

Rocky Mountain Flora. By WILLIAM A. WEBER. vii + 438 pp., 346 figs., 8 color plates. Colorado Associated University Press, Boulder. 1972.

This is the fourth edition of a book originally published in 1953 under the title *Handbook of Plants of the Colorado Front Range*. The third edition was the first in this family of handbooks to bear the title *Rocky Mountain Flora* and was reviewed in 1969 by W. R. Ernst with views essentially in accordance with my own (Madroño 20:29-30). In interest of economy of space the reader is referred to that review.

The new edition sports an attractive new cover with a nice photograph of the ever popular *Calypto bulbosa*. Inside, near the front, 8 pages of color photos by the author and H. W. Roberts have been inserted, some of which are very good. The pages have been trimmed to narrower margins, the corners have been rounded, and thinner but good grade paper has been used. Thus the overall size of the book has been reduced, making it considerably more convenient to carry into the field.

The new edition is essentially a reprint of the previous one with nomenclatural changes in some genera, such as in *Betula*, *Helianthus*, and *Heterotheca*, and the addition of some species, as in *Phlox*. Other changes may have been made but they are inconspicuous. The drawings by C. F. Yocum are reproduced with less loss of detail than in the third edition, but many are still too black. The book is remarkably error-free; the labels on the *Phleum* illustrations are no longer reversed.

The book nicely bridges the needs of the beginner, the amateur, and the professional. Introductory remarks and instructions are directed largely toward the beginner, the keys generally use easily seen characters, common synonyms are given for many species, and an attempt has been made to be complete for the region covered. The book is highly usable for all interested in the flora of the Rocky Mountain region, over an area considerably greater than the Colorado Front Range, which it is specifically covers.—RICHARD SPELLENBERG, Department of Biology, New Mexico State University, Las Cruces 88001.

The Quantitative Analysis of Plant Growth. By G. CLIFFORD EVANS. xxvi + 734 pp. University of California Press, Berkeley, 1972. \$22.00.

This monograph is directed toward ecologists and others interested in quantitatively describing plant growth under natural conditions. It represents Volume 1 in a series entitled "Studies in Ecology" and is presented on an advanced undergraduate or beginning graduate level. A recurring theme throughout the book is the "ontogenetic drift" of an individual plant as it experiences different environments over its lifetime. Such changes in plant form and function are discussed mainly in the restricted sense of effects on the dry weight or the area of plant tissues. Considerable

attention is also given to the effect of various environmental factors like temperature or illumination level on plant growth under controlled conditions in relation to analogous observations in the field.

The first 51 pages serve as an introduction to the growth and development of plants. Physiological and structural problems such as what fraction of total plant photosynthesis takes place in the stem, the influence of sunflecks on leaf temperature, and the persisting effects of past environment are introduced as a prelude to the more quantitative account to follow.

Part II comprises 134 pages on designing experiments and collecting data. The basic premise is that a statistically appropriate number of plants should be harvested at suitable intervals from a uniform population of plants. Variability can be reduced by seed and soil selection as well as by use of growth chambers. Measurements of environmental parameters under natural conditions and of lengths, areas, and fresh as well as dry weights of plant parts are discussed. Ingenious ways of measuring leaf area are presented, but little attention is paid to root surface area. A few precautions (such as using temperatures near 80°C) are noted for obtaining accurate dry weights. Although a chapter is devoted to the determination of the CO₂ evolution accompanying respiration, there is no comparable coverage of photosynthesis or photorespiration.

Part III presents 231 pages on the statistical analysis of data with respect to certain basic relations. For instance, the "Relative Growth Rate [$d \ln (\text{plant dry weight})/dt$] equals the "Leaf Area Ratio" (leaf area/plant dry weight) times the "Unit Leaf Rate" [$d (\text{plant dry weight})/dt \times 1/\text{leaf area}$]. Both Leaf Area Ratio and Unit Leaf Rate are further factored into a pair of contributing quantities. Ways to recognize and remove "whole sections of corrupt data" caused by an accident during an experiment are presented from a statistical point of view. Linear, exponential, and other relations between leaf area, leaf dry weight, plant dry weight, and seed dry weight are discussed; data on various species like *Helianthus annuus* and *Impatiens parviflora* are used, especially with regard to the influence of environmental factors on the amount and distribution of dry weight.

Part IV covers 169 pages aptly titled, "Problems Posed by the Growing Plant." The fraction of the plant dry weight in the leaves is compared for various species under different conditions, e.g., vermiculite vs. natural soil. Aspects of developmental anatomy of roots, stems, and leaves are introduced and then related to physiological observations and environmental influences. Resistances for gaseous exchanges by leaves are briefly discussed as are growth measurements on plants selected to serve as biological integrators of environmental conditions. Problems of analysis of respiration and of dry matter production in an entire ecosystem, including the part below ground level, are considered. Appreciable space is devoted to suggestions for future research, such as measuring photosynthesis, photorespiration, and respiration under field conditions. Experiments on plant growth bridging the gap between the natural environment and that of the growth chamber are encouraged.

The appendices extend over 51 pages primarily on the Thoday respirometer plus a section printed on colored paper for ease of reference. A bibliography (20 pages long) covers much of the older literature and it is followed by a rather unconventional 74-page index. Neither the Table of Contents nor the Index use page numbers, but instead refer to the material by section number.

Although authoritative and clearly written, the book is extremely verbose, the Preface alone rambling along for 11 pages. Sometimes the wordiness is a consequence of giving a myriad of details on each of a series of experiments or by repeatedly cautioning against a too simpleminded interpretation of the data; both aspects can serve a purpose and reflect the extensive experience that the author has had in the area of plant growth analysis. At other times, the extra words are used for a historical diversion or a generally pertinent and sometimes droll comment, e.g., "Plants are organisms very inaccessible to the human mind."—PARK S. NOBEL, Department of Biology, University of California, Los Angeles 90024

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THE NORTH AMERICAN SPECIES OF *VULPIA* (GRAMINEAE)

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The grass genus *Vulpia* comprises approximately 25 species native to temperate and subtropical regions of Europe, the Mediterranean region, and North and South America. Several species have been introduced into Asia and Australia. In the warmer regions these grasses grow only during the cool season or at high elevations. Of the five North American species two are introduced and the others are native.

Piper (1906), Hitchcock (1935), and Chase (1951) grouped the American species of *Vulpia* in *Festuca*. Others, including Bews (1929), Henrard (1937), Fernald (1945, 1950), Chippendall (1955), Parodi (1956), Paunero (1964), Hubbard (1968), and Rosengurt et al. (1970) have accorded *Vulpia* generic rank.

The present investigation was undertaken to determine the taxonomic relationships of the five species of *Vulpia* native to or adventive in North America. Of special concern were patterns of variation within populations of the widespread west coast species, *V. microstachys*.

GROSS MORPHOLOGY

Species of *Vulpia* characteristically are short-lived annuals. Morphological characters selected as having most diagnostic value in the delimitation of species are the general conformation of the inflorescence (pedicels and panicle branches erect or spreading), spikelet length, number of florets per spikelet, relative lengths of the glumes, length of the lowermost floret, and length of the lemma awn of lowermost floret. Spikelet indument is the primary character utilized in the delimitation of varieties.

ANATOMY — HISTOLOGY

In transverse section the culm internodes of the five species of *Vulpia* examined follow the general cellular pattern described by Metcalfe (1960) for *Festuca arundinacea* Schreb. The internodes have a large central cavity bordered by thin-walled parenchyma cells. Vascular bundles are arranged in an outer ring of small bundles embedded in the sclerenchyma of the cortex and an inner ring of larger bundles located in the ground tissue of the "pith" area. Surrounding all vascular bundles is a single ring of sheath cells.

Examination of the internal anatomy of the leaf blade of the five North American species of *Vulpia* confirmed previous reports that these are "festucoid". In all material examined the bundle sheaths are double, with the cell walls of the inner sheath radially thickened. The outer sheath cells are large and thin-walled. Chlorenchyma cells of the mesophyll are loosely and irregularly arranged. Clusters of small, thick-walled sclerenchyma cells are associated both adaxially and abaxially with the larger vascular bundles of the leaf. Sclerenchyma cells are not associated with the smaller vascular bundles.

The adaxial blade surface exhibits well developed ribs. Each rib is comprised of a single vascular bundle and associated supporting cells. The vascular bundles are separated by deep U-shaped furrows. Bulliform cells at the base of the furrow are fan-shaped in *V. myuros* var. *hirsuta*, *V. bromoides*, and *V. octoflora* var. *octoflora*, irregular in varieties of *V. microstachys*, and only slightly different from other epidermal cells in *V. myuros* var. *myuros*. Differences in bulliform cells provide a diagnostic feature for separation of *V. myuros* var. *myuros* from *V. myuros* var. *hirsuta*.

Leaf epidermis features of *Vulpia* taxa were found to be typically festucoid and essentially the same as for the species of *Festuca* reported on by Metcalfe (1960). The short cells in the epidermis over the vascular bundles are solitary or paired, microhairs are absent, and the silica bodies are round or elliptical. The silica cells generally are adjacent to cork cells and appear to fit into concavities in the thick-walled cork cells. Long cells in the intercostal region have slightly sinuous walls. Stomata predominantly are on the abaxial surface and are generally arranged in regular rows. Subsidiary cells of the stomata are dome-shaped. The leaf epidermis of *V. sciurea* is noticeably different from that of the other species studied in that the stomata are relatively more abundant and the long cells of the intercostal zones are narrower.

CYTOLOGY

The basic chromosome number for *Vulpia* is $x = 7$. All North American species are either diploid ($2n = 14$) or hexaploid ($2n = 42$), but several European species have been reported to be tetraploid ($2n = 28$). Aneuploidy has not been reported for the genus.

Previous chromosome records for taxa present in North America are as follows: *Vulpia bromoides*, $2n = 14$, Stahlin, in Darlington and Wylie, 1956; Myers, 1947, Löve and Löve, 1948, Hedberg, 1957; *V. octoflora* var. *octoflora*, $2n = 14$, Gould, 1958; *V. octoflora* var. *hirtella*, $2n = 14$, Bowden and Senn, 1962; *V. myuros* var. *myuros*, $2n = 14$, Litardiere, in Darlington and Wylie, 1956; $2n = 42$, Litardiere, 1950, Gould 1966; *V. myuros* var. *hirsuta*, $2n = 42$, Gould, 1960, reported as *Festuca megalura*; *V. microstachys*, $2n = 42$, Niehaus, 1961, counts for plants referable to all recognized varieties of the species.

The following 38 chromosome counts were made in the present study. Counts for *Vulpia sciurea*, *V. microstachys* var. *pauciflora*, and *V. m.* var. *ciliata* were from mitotic preparations, all others were from meiotic divisions. The record for *V. sciurea* is the first for the taxon. Unless otherwise indicated, the collections cited are those of R. I. Lonard. Voucher specimens are deposited in TAES.

Vulpia octoflora var. *octoflora*. $2n = 14$. OKLAHOMA. Logan Co.: 2311. TEXAS. Brazos Co.: 1888. Henderson Co.: 2300. Jasper Co.: 2092. Leon Co.: 2056, 2108. Liberty Co.: 2079. Newton Co.: 2089. Robertson Co.: 2054, 2107. Van Zandt Co.: 2070.

Vulpia octoflora var. *glauca*. $2n = 14$. KANSAS. Chase Co.: 2376. Jefferson Co.: 2359. McPherson Co.: 2322. Reno Co.: 2336. TEXAS. Austin Co.: 2015. Kendall Co.: Waller 1923. Llano Co.: 2204. Mason Co.: Waller 1899.

Vulpia octoflora var. *hirtella*, $2n = 14$. ARIZONA. Graham Co.: 2268. Pinal Co.: 2249. Santa Cruz Co.: 2220. TEXAS. Atascosa Co.: 2273. Wilson Co.: 2022.

Vulpia sciurea. $2n = 42$ (mitotic preparations). TEXAS. Bexar Co.: Waller 1929. Brazos Co.: 2197.

Vulpia myuros var. *myuros*. $2n = 42$. TEXAS. Angelina Co.: 2095. Bowie Co.: 2116. Cherokee Co.: 2074. Hunt Co.: 2121. Leon Co.: 2109. Van Zandt Co.: 2067.

Vulpia myuros var. *hirsuta*. $2n = 42$. TEXAS. Brazos Co.: 2075. Hopkins Co.: 2120. Marion Co.: 2114.

Vulpia microstachys var. *simulans*. $2n = 42$ (mitotic preparations). ARIZONA. Pinal Co.: 2254. Gila Co.: 2258.

Vulpia microstachys var. *ciliata*. $2n = 42$ (mitotic preparations). ARIZONA. Graham Co.: 2269.

TAXONOMY

VULPIA K.C. Gmelin, Fl. Baden. 1:8. 1805. TYPE SPECIES: *Vulpia myuros* (L.) K.C. Gmelin.—*Festuca* L. subg. *Vulpia* (K.C. Gmelin) Hackel, in Engler and Prantl, Nat. Pflanzenfam. 2:75. 1887.

Annuals (the North American species), with weak, erect or decumbent culms, these branching only or mainly at the base. Sheaths rounded, glabrous or pubescent. Ligules membranous, usually less than 1 mm long. Blades thin, narrow, flat or loosely involute. Inflorescence a narrow panicle with stiff, appressed or spreading branches or reduced to a spicate raceme. Spikelets laterally compressed, with (1-) 2-17 florets, the uppermost reduced. Disarticulation above glumes and between florets. Glumes subulate, the first 1-nerved, the second 3-nerved. Lemmas lanceolate or acuminate, 5-nerved, mucronate or with an awn to 2 cm or more long. Paleas translucent, glabrous or pubescent near the margins, usually slightly shorter than and partially enclosed by the lemmas. Stamens one or occasionally three in chasmogamous plants.

Anthers 0.3–1.5 mm long. Caryopses narrow, elongate, attenuate, flattened dorso-ventrally with the margins incurving at maturity; embryo small, one-fifth to one-tenth as long as the endosperm. Basic chromosome number, $x = 7$.

The separation of *Vulpia* from *Festuca* is based on a number of characters. With a few exceptions, the species of *Vulpia* are short-lived annuals, whereas those of *Festuca* are strong perennials. Typically the anthers of *Vulpia* are less than 0.5 mm long and the plants are cleistogamous. In *Festuca* the anthers are 3 mm or more long and the plants are chasmogamous. Species of *Vulpia* primarily are "weedy" grasses of disturbed habitats. In contrast, the festucas mainly are economically important grasses of meadows and pasturelands.

KEY TO THE SPECIES

First glume more than $\frac{1}{2}$ the length of second glume.

Lemma of lowermost floret 2.5–3.5 mm long, pubescent; caryopses 1.5–2.0 mm long. 2. *V. sciurea*

Lemma of lowermost floret 3.5–7.5 mm long, pubescent, scabrous or glabrous; caryopses 2.5–5.5 mm long.

Spikelets with 5–11 (–17) florets; florets closely imbricate, with rachilla internodes typically 0.5–0.7 mm long; lemma awns 0.3–6.0 (–9.0) mm long. 1. *V. octoflora*

Spikelets with 1–5 (–7) florets, the florets not closely imbricate, with rachilla internodes usually 1 mm or more long; lemma awns 4–22 mm long.

Panicle branches and pedicels, at least the basal one, spreading or reflexed at maturity and with a callus in the branch axil. 3. *V. microstachys*

Panicle branches and pedicels appressed-erect or the branches spreading at the tips from an erect base; branches and pedicels all lacking axillary calluses. 4. *V. bromoides*

First glume less than $\frac{1}{2}$ the length of second glume, usually much reduced and often rudimentary. 5. *V. myuros*

1. *VULPIA OCTOFLORA* (Walt.) Rydb., Bull. Torrey Bot. Club 36:528. 1909.

Annual with slender, weak, erect or decumbent culms, these mostly 10–60 cm tall, solitary, or loosely tufted. Culms and leaves glabrous or pubescent. Ligules 0.5–1.0 mm long. Blades narrow, flat, or involute, to 10 cm long, 0.5–1.0 mm broad, soon withering and turning brown. Panicles narrow, 1–20 cm long, with appressed, spicate or racemose branches or reduced to a spicate raceme. Spikelets with 5–17 florets, green or straw colored at maturity, laterally compressed, 4–10 mm long excluding the awns. Glumes subulate, the first 1-nerved, 1.7–4.5 mm long, the second 3-nerved, 2.7–6.7 mm long. Lemma of lowermost floret 2.7–6.5 mm long excluding the awn, lanceolate, glabrous, scabrous, or

pubescent, with an awn 0.3–6.0 (–9.0) mm long. Paleas translucent and pubescent near the margins, slightly shorter than the lemmas. Stamens one, occasionally three in chasmogamous plants. Anthers 0.3–1.5 mm long, borne on short filaments and usually clustered at the apex of the ovary between the two plumose stigmas. Caryopses brown at maturity, 1.7–3.3 mm long. Embryos about 0.3 mm long, inconspicuous.

Piper (1906) noted considerable variability in *Vulpia octoflora* but considered the differences between the variants too inconsistent for the recognition of more than two varieties. Fernald (1932), Steyermark (1963), and others have recognized a number of varieties, based on morphological divergence and geographical segregation. Some slight variation of general nature is apparent between plants and populations of *V. octoflora* in the Southeastern States and those of other regions of North America. In North Carolina, South Carolina, Georgia, and northern Florida, the plants tend to be more robust and the inflorescence more open than in populations of northern and western North America. The southeastern plants also have longer spikelets with more florets, longer caryopses, and quite consistently glabrous lemmas. Furthermore, the awn of the lowermost floret usually is longer.

Recognition of the following three varieties of *V. octoflora* is not entirely satisfactory. The characteristics of small spikelet size and short awns that provide the basis for the delimitation of var. *glauca* do not appear correlated in all cases. Depauperate plants of the Southwest with small spikelets fall within the range of var. *glauca* but the lemmas often are densely pubescent—the distinguishing characteristic of var. *hirtella*. Lemma indument often varies on spikelets of the same plant and even on different lemmas of the same spikelet.

KEY TO VARIETIES OF VULPIA OCTOFLORA

Spikelets, excluding awns, mostly 4.0–5.5 mm long; awn of lowermost floret 0.3–3.0 mm long. 1B. var. *glauca*

Spikelets, excluding awns, mostly 5.5–10.0 mm long; awn of the lowermost floret 2.5–6.0 (–9.0) mm long.

Lemma glabrous or slightly scabrous on back, often scabrous on margins. 1A. var. *octoflora*

Lemma prominently long-scabrous to densely pubescent on back, at least near apex. 1C. var. *hirtella*

1A. *VULPIA OCTOFLORA* (Walt.) Rydb. var. *OCTOFLORA*.—*Festuca octoflora* Walt., Fl. Carol. 81. 1788. TYPE: South Carolina, Santee Valley, *Walter s.n.* The location of the type apparently is unknown. Piper (1906) stated that according to A. S. Hitchcock there is no specimen to represent this species in the part of Walter's herbarium preserved in the British Museum.—*Gnomia octoflora* (Walt.) Lunnell, Amer. Midl. Naturalist 4:224. 1915.

Festuca setacea Poir., Encyl. Suppl. 2:638. 1811. TYPE: South Carolina (?). Described from a plant grown in the Jardin du Val de Grace, France, the original source not definitely known. Piper (1906) did not locate the type nor have we done so.—*Diarrhena setacea* (Poir.) Roem. & Schult., Syst. Veg. 1:289. 1817.

Festuca parviflora Ell., Bot. So. Carolina & Georgia 1:170. 1816. TYPE: South Carolina, Orangeburg, *Mrs. J. S. Bennett s.n.* The type is at the College of Charleston *vide* Piper (1906); it was examined by Piper but not by us.

Festuca octoflora Walt. var. *aristulata* L. H. Dewey, Contr. U. S. Natl. Herb. 2:547. 1894. TYPE: "Dry hills throughout Texas and common throughout the southern United States". No collection cited.

Inflorescence with slender lower branches spreading at the tips or the branches all contracted and racemose. Spikelets 5.5–10.0 mm long, usually not or only slightly overlapping. Lemmas glabrous or somewhat short-scabrous near apex and on margins. Awn of lowermost floret 3–6 (–9) mm long. Caryopses 2.0–3.7 mm long.

DISTRIBUTION: Widespread throughout North America and introduced in temperate regions of South America, Europe, and Asia. Usually in disturbed habitats such as old fields, roadsides, ditches, and other areas where secondary plant succession is occurring. In North America, *V. octoflora* var. *octoflora* ranges from Connecticut to British Columbia and southward to Florida and Baja California. It is most commonly encountered from Virginia to northern Oklahoma and southward to northern Florida and the Texas Gulf Prairie.

1B. *VULPIA OCTOFLORA* (Walt.) Rydb. var. *GLAUCA* (Nutt.) Fern., Rhodora 47:104. 1945.—*Festuca tenella* Willd. var. *glauca* Nutt., Trans. Amer. Philos. Soc. 5:147. 1837. TYPE: Arkansas, Fort Smith, *Nuttall s.n.* (PH).—*Festuca octoflora* Walt. var. *glauca* (Nutt.) Fern., Rhodora 34:209. 1932.

Festuca tenella Willd., Sp. Pl. 1:419. 1797. TYPE: "Habitat in America boreali". Willdenow made no reference to a specific (type) collection.—*Schenonorus tenella* (Willd) Beauv., Ess. Agrost. 99, 163, 177. 1812.—*Brachypodium festucoides* Link, Enum. Pl. Hort. Berol. 1:95. 1821. Based on *Festuca tenella* Willd.—*Vulpia tenella* (Willd.) Heynh., Nom. 1:854. 1840.—*Festuca octoflora* Walt. var. *tenella* (Willd.) Fern., Rhodora 34:209. 1932.—*Vulpia octoflora* (Walt.) Rydb. var. *tenella* (Willd.) Fern., Rhodora 47:107. 1945. *Festuca gracilentia* Buckl., Proc. Acad. Nat. Sci. Philadelphia 1862:97. 1862. TYPE: "Northern Texas", *Buckley s.n.* (PH).

Panicle branches usually appressed, only infrequently spreading at the tips. Spikelets mostly 4.0–5.5 mm long excluding the awns, sessile or short-pedicelled, closely arranged on main inflorescence axis and short branches. Lemmas glabrous or scabrous. Awn of lowermost floret 0.3–3.0 mm long.

DISTRIBUTION: Widespread in North America. Most frequent in southern Canada and the northern half of the United States, ranging from southern Quebec, Ontario, and British Columbia to northern Georgia and California. Variety *glauca* is the most common representative of *V. octoflora* from Maine and North Dakota to Virginia and western Kansas.

Fernald (1932) followed Nuttall in recognizing *V. octoflora* var. *glauca* as a varietal taxon, which he characterized as having crowded inflorescences, imbricated spikelets, and awns not more than 2 mm long. Fernald also proposed varietal status under *V. octoflora* for Willdenow's *Festuca tenella*. In the present study, however, the characteristics of *glauca* and *tenella* were found to vary and intergrade to such an extent that taxonomic recognition of the latter would be highly unsatisfactory.

Plants of many populations from the Texas Panhandle are intermediate in morphological characters between var. *octoflora* and var. *glauca*. In these plants the panicle branches are appressed, the spikelets are about 5.5 mm long and densely overlapping, and the awns of the lowermost florets are less than 3 mm long.

1C. VULPIA OCTOFLORA var. HIRTELLA (Piper) Henr., Blumea 2:320. 1937.—*Festuca octoflora* subsp. *hirtella* Piper, Contr. U. S. Natl. Herb 10:12. 1906. TYPE: Arizona, Pima Co., Santa Catalina Mts., Shear 1962 (US).

Festuca pusilla Buckl., Proc. Acad. Nat. Sci. Philadelphia 1862:98. 1862. TYPE: "Upper California", Nuttall s.n. (PH).

Panicle branches appressed, densely-flowered, the spikelets closely overlapping. Spikelets mostly 5.5–10.0 mm long excluding the awns. Lemmas prominently scabrous to densely pubescent. Awn of lowermost floret 2.5–6.5 mm long.

DISTRIBUTION: British Columbia south to Oklahoma, Texas, and Baja California. This is the most common variety of *V. octoflora* in the Southwest. A few plants of southeastern U. S. with strongly scabrous lemmas have been referred to this taxon.

2. VULPIA SCIUREA (Nutt.) Henr., Blumea 2:323. — *Festuca sciurea* Nutt., Trans. Amer. Philos. Soc. 5:147. 1837. TYPE: Arkansas, Nuttall s.n., in 1837 (PH).

?*Festuca quadriflora* Walt., Fl. Carol. 81. 1788. No known type or authentic specimen and description inadequate for determination of species. Not *Festuca quadriflora* Honck., 1782.

Festuca monandra Ell., Bot. So. Carolina & Georgia 1:170. 1816. Published as a synonym of *Festuca myuros* as misapplied by Elliot. In referring to the "hairy corolla" Elliott indicated that the plant he had in mind was *Vulpia sciurea*.—*Dasiola elliottea* Raf., Noegenyt. 4. 1825. Based on *Festuca monandra* Ell.—*Vulpia elliottea* (Raf.) Fern., Rhodora 47:106. 1945.

Culms 15–60 cm tall, erect or drooping at maturity. Herbage glabrous. Ligules 0.5–1.0 mm long. Blades flat or involute, usually less than 10 cm long and 0.5–1.0 mm broad. Panicles contracted, 5–20 cm long, with erect-appressed branches. Spikelets laterally compressed, 3.5–5.0 mm long excluding the awns, with 3–6 florets, the uppermost reduced. Glumes glabrous, subulate, the first 1-nerved, 1.3–2.5 mm long, the second obscurely 3-nerved, 2.5–4.0 mm long. Lemma of lowermost floret lanceolate, appressed-pubescent, 2.5–3.5 mm long excluding the awn. Awn of lowermost floret 4.5–9.5 mm long. Palea slightly shorter than the lemma. Stamens one, with an anther about 0.5 mm long on a short filament. Caryopses cylindrical and attenuate, 1.5–2.0 mm long, with a short, inconspicuous embryo.

DISTRIBUTION: South on the eastern Coastal Plain from New Jersey and Delaware to northern Florida, southern Alabama and Mississippi, a few records from southern Iowa, northern Missouri and central Oklahoma, and many collections from the eastern half of Texas. *Vulpia sciurea* grows mostly in deep sandy soil of open woodlands, field borders and roadside ditches. It is perhaps the most distinct of the North American species of the genus, readily differentiated from other vulpias by its small spikelets and consistently pubescent florets. Although rather wide ranging, this species is neither abundant nor conspicuous in areas of occurrence.

3. *VULPIA MICROSTACHYS* (Nutt.) Benth., Pl. Hartw. 342. 1957.

Culms solitary or loosely tufted, glabrous or puberulent. Sheaths and blades glabrous or pubescent, the blades involute or less frequently flat, mostly 10 cm or less long and 0.5–1.0 mm broad. Ligules 0.5–1.0 mm long. Panicles narrow, 3–13 cm long, the branches and pedicels at first erect-appressed and then at least the lowermost typically spreading or reflexed in age; sometimes all pedicels and branches spreading or reflexed at maturity. Spikelets 4–9 mm long excluding the awns, often purple-tinged, with 1–6 florets, the uppermost reduced and inconspicuous. Glumes glabrous, scabrous, or pubescent, subulate, the first 1.7–5.5 mm long, the second 3.5–7.5 mm long. Lemma of lowermost floret (3.5–) 4.5–7.0 mm long excluding the awn, indistinctly 5-nerved, glabrous, scabrous or pubescent. Awn of lowermost floret (3–) 6–20 mm long. Palea usually slightly longer than body of lemma, tipped by 2 short, scabrous awns. Stamens usually 1, occasionally 3. Caryopses 3.5–5.5 mm long.

Several species have been delimited on the basis of populations herein interpreted as comprising *V. microstachys*. Piper (1906) recognized seven specific segregates, basing these on spikelet pubescence, the relative degree of spreading inflorescence branches, and the number of florets per spikelet. Hitchcock (1923, 1935) and Chase (1951) followed closely the concepts of Piper and recognized seven, eight, and nine

species respectively. The four varieties herein recognized all are differentiated on the basis of spikelet indument. The varieties commonly grow intermingled and intermediate, intergrading types are not infrequent.

KEY TO VARIETIES OF VULPIA MICROSTACHYS

Spikelets pubescent.

Glumes or lemmas glabrous.

Lemmas pubescent; glumes glabrous. . . . 3A. var. *microstachys*

Lemmas glabrous; glumes pubescent. . . . 3C. var. *confusa*

Glumes and lemmas pubescent. . . . 3B. var. *ciliata*

Spikelets glabrous or scabrous. . . . 3D. var. *pauciflora*

3A. *VULPIA MICROSTACHYS* (Nutt.) Benth. var. *MICROSTACHYS*.—*Festuca microstachys* Nutt., J. Acad. Nat. Sci. Philadelphia II, 1:187. 1848. TYPE: California, Los Angeles, *Gambel s.n.* The type has not been located; Piper (1906) noted that it is not at Kew nor in the Philadelphia Academy of Science.

Festuca microstachys Nutt. var. *subapressa* Suksdorf, Werdenda 1:3. 1923. TYPE: Washington, Klickitat Co., Bingen, *Suksdorf 6236* (lectotype in WS, isotypes in K, WS).

Festuca arida Elmer, Bot. Gaz. (Crawfordsville) 26:52–53. 1903. TYPE: Washington, Yakima, *Henderson 2196* (isotypes in US, WS).—*Vulpia arida* (Elmer) Henr., Blumea 2:323. 1937.

Panicle branches and pedicels all spreading or reflexed or only the basal ones spreading. Spikelets 4.5–7.5 mm long excluding the awns, with (1–) 2–5 florets. Glumes glabrous. Lemmas sparsely to densely pubescent.

DISTRIBUTION: Occasional in loose soil on open slopes, ditchbanks and road rights of way, from northern Idaho, Washington, Oregon, and western Nevada to southern California.

Plants with inflorescence branches and pedicels only slightly spreading at maturity have been recognized as *Vulpia arida* (Elmer) Henr.

3B. *Vulpia microstachys* (Nutt.) Benth. var. *ciliata* (Beal) Lonard & Gould, comb. nov.—*Festuca microstachys* Nutt. var. *ciliata* Beal, Grasses N. Amer. 2:585. 1896. Not *Festuca ciliata* Danth. TYPE: Oregon, Grants Pass, *Howell s.n.* (holotype in MSC, isotype in US).—*Festuca microstachys grayi* Abrams, Fl. Los Angeles 52. 1904. Based on *Festuca microstachys* Nutt. var. *ciliata* Beal.—*Festuca pacifica* Piper var. *ciliata* (Beal) Hoover, Madroño 3:227. 1936.—*Festuca grayi* (Abrams) Piper, Contr. U. S. Natl. Herb. 10:14. 1906.—*Vulpia grayi* (Abrams) Henr., Blumea 2:323. 1937.

Festuca eastwoodae Piper, Contr. U.S. Natl. Herb. 10:16. 1906. TYPE: California, Monterey Co., Santa Lucia Mts., *Eastwood s.n.*, in 1897 (holotype in US).—*Vulpia eastwoodae* (Piper) Henr. Blumea 2:323. 1937.

Panicle branches and pedicels all spreading or reflexed or the upper ones erect. Florets usually 2–4. Glumes and lemmas sparsely or densely pubescent.

DISTRIBUTION: In loose, sandy soils from central Washington through Oregon and California to northern Baja California and western Arizona.

This is the second most common variety of *V. microstachys* in California, exceeded in abundance and distribution only by var. *pauciflora*. Plants of forest openings in northern California with all branches and pedicels strongly reflexed or spreading and spikelets densely pubescent have been recognized as *Vulpia eastwoodae* (Piper) Henr.

3C. ***Vulpia microstachys*** (Nutt.) Benth. var. ***confusa*** (Piper) Lonard & Gould, comb. et stat. nov. — *Festuca confusa* Piper, Contr. U. S. Natl. Herb. 10:13. 1906. TYPE: Washington, Klickitat Co., *Suksdorf 1140* (holotype in US, isotypes in UC, WS). — *Vulpia confusa* (Piper) Henr., Blumea 2:323. 1937.

Festuca suksdorfii Piper ex Suksdorf, Werdenda 1:2. 1923. TYPE: Washington, Klickitat Co., Bingen, *Suksdorf 5604* (lectotype and isotype in WS).

Festuca tracyi Hitchc. in Abrams, Illustr. Fl. Pacific States 1:220. 1923.

TYPE: California, Napa Co., *Tracy 1479* (isotypes in CAS, UC).

—*Vulpia tracyi* (Hitchc.) Henr., Blumea 2:323. 1937.

Panicle branches and pedicels all spreading or reflexed at maturity or the upper ones erect.

DISTRIBUTION: Occasional on sandy, open sites from southern Washington to southern California.

Vulpia microstachys var. *confusa* apparently is the least abundant of the four *V. microstachys* varieties. A form with all branches and pedicels widely spreading or reflexed was described by Hitchcock as *Festuca tracyi*.

3D. ***Vulpia microstachys*** (Nutt.) Benth. var. ***pauciflora*** (Beal) Lonard & Gould, comb. nov.—*Festuca microstachys pauciflora* Beal, Grasses N. Amer. 2:586. 1896. TYPE: Oregon, *Howell s.n.*

Festuca reflexa Buckl., Proc. Acad. Nat. Sci. Philadelphia 1862:98. 1862. TYPE: "Upper California", *Nuttall s.n.* (PH).—*Vulpia reflexa* (Buckl.) Rydb., Bull. Torrey Bot. Club 36:538. 1909.

Festuca pacifica Piper, Contr. U. S. Natl. Herb. 10:12. 1906. TYPE: Washington, Whitman Co., Pullman, *Elmer 262* (US).—*Vulpia pacifica* (Piper) Rydb., Bull. Torrey Bot. Club 36:535. 1909.

Festuca subbiflora Suksdorf, Werdenda 1:2. 1923. TYPE: Washington, Klickitat Co., *Suksdorf 6144* (lectotype in WS, isotypes in CAS, K, WS), *10299* (CAS, K), and *1298*.

Festuca dives Suksdorf, Werdenda 1:3. 1923. Not *Festuca dives* Muell., 1863. TYPE: Washington, Klickitat Co., Bingen, *Suksdorf 6153* (lectotype in WS, isotypes in CAS, WS).

Festuca pacifica Piper var. *simulans* Hoover, Madroño 3:228. 1936.

TYPE: California, Kern Co., Blackwells Corner, *Hoover 451* (UC).

—*Festuca microstachys* Nutt. var. *simulans* (Hoover) Hoover, Leaflet. W. Bot. 10:338–339. 1966.

Panicle branches and pedicels all spreading or reflexed or the upper ones erect. Spikelets with 1–6 florets.

DISTRIBUTION: On sandy, often disturbed sites from British Columbia and western Montana southward to Arizona and Baja California.

This is the most common and widespread variety of the species. It often grows intermingled with plants of the other varieties. Differences in spikelet indument among the four varieties usually are in sharp contrast but intermediacy is expressed in some populations, both in respect to length and density of hairs or spicules. Specimens of the type collection of *Festuca divisa* have short- to long scabrous lemmas and thus are essentially intermediate between the varieties *pauciflora* and *ciliata*. The name *Vulpia reflexa* has been applied to plants with sharply reflexed, 1–2 (–3) -flowered, glabrous spikelets. Difficulty is experienced in the separation of immature or atypical plants of *V. microstachys* var. *pauciflora* and *V. bromoides*. In southern California and Baja California, differences between var. *microstachys* and *V. octoflora* var. *octoflora* are not always apparent.

4. VULPIA BROMOIDES (L.) S.F. Gray, Natur. Arrange. Brit. Plants 124. 1821.—*Festuca bromoides* L., Sp. Pl. 1:75. 1753. TYPE: Italy, "In Anglia Gallia".

Bromus dertonensis All., Fl. Pedem 2:249. 1785. TYPE: Italy, *Scheuchzer s.n.*—*Festuca dertonensis* (All.) Asch. & Graebn., Syn. Mittleleur. Fl. 2:588. 1900.—*Vulpia dertonensis* (All.) Gola, Malpighia 18:366. 1904.

Festuca sciuroides Roth, Bet. Abh. & Beobacht. 43. 1787. TYPE: Germany.—*Vulpia sciuroides* (Roth) K.C. Gmelin, Suppl. Fl. Baden 66. 1826.

Culms solitary or loosely tufted, erect or decumbent at base, glabrous or minutely retrorsely scabrous-pubescent, 5–50 cm tall. Leaves glabrous or puberulent. Ligules about 0.5 mm long. Blades flat or involute, mostly less than 15 cm long and 0.5–2.5 mm broad. Panicles contracted, 5–15 cm long, the branches usually tightly erect-appressed; panicles conspicuously exserted above uppermost leaf, the inflorescence stalk extending as much as 15 cm long below the lowermost branches. Pedicels flattened or noticeably clavate above. Spikelets 5–10 mm long excluding the awns, with 4–7 florets, the uppermost reduced; nodes of rachilla about 1 mm apart, the florets appearing widely spaced. Glumes glabrous, subulate, the first 3.5–5.0 mm long, the second 4.5–7.0 mm long. Lemma of lowermost floret (4.0–) 5.5–8.0 mm long excluding the awn, glabrous and lustrous or scabrous. Awn of lowermost floret 3–12 mm long, firm,

scabrous. Palea about as long as lemma. Stamens usually one, with an anther about 0.5 mm long. Caryopses 3.5–4.0 mm long.

DISTRIBUTION: In temperate regions of the world, common throughout Europe. *Vulpia bromoides* is adventive or naturalized in North and South America and is an introduced “weedy” grass of high altitudes in tropical Africa. In North America it is most common on the west coast where it ranges from British Columbia to northern Baja California. It occurs sparingly in other regions of North America.

Vulpia bromoides is similar in general habit and spikelet characteristics to *V. myuros* but is readily distinguished by the longer first glume. As has been noted, immature or depauperate specimens can be confused with similarly atypical plants of *V. microstachys* var. *pauciflora*.

5. VULPIA MYUROS (L.) K. C. Gmelin, Fl. Baden. 1:8. 1805.

Culms solitary or loosely tufted, erect or ascending from a decumbent base, glabrous, 10–60 (–90) cm tall. Sheaths glabrous or the lowermost puberulent, broadly rounded and often lobed laterally at apex, abruptly narrowing to and continuous with a fimbriate ligule less than 0.5 mm long. Blades long or short, flat or more commonly involute, often filiform, mostly 15 cm or less long and 0.5–3.0 mm broad, usually glabrous on abaxial surface and thinly puberulous on adaxial surface, at least near base. Inflorescence a contracted, often rather dense panicle or spicate raceme 3–25 cm long, often not completely exerted from sheath at maturity; panicle branches erect-appressed or drooping. Spikelets 5.5–12.0 mm long excluding the awns, with 3–7 florets. Glumes thin, glabrous, subulate, the first mostly 0.5–2.5 mm long, the second 3-nerved, 2.3–5.5 mm, at least twice as long as the first. Lemma of lowermost floret 4.5–7.0 mm long excluding the awn, usually scabrous above; lemma awns 7.5–22.0 mm long. Palea about as long as lemma, membranous, colorless, glabrous. Stamens usually 1, the anther about 0.5 mm long. Caryopses 3.0–4.5 mm long.

KEY TO VARIETIES OF VULPIA MYUROS

- Lemmas not ciliate on margins near apex; awn of lowermost floret 7.5–17.0 mm long. 5A. var. *myuros*
 Lemmas ciliate on margins near apex; awn of lowermost floret 9.5–22.0 mm long. 5B. var. *hirsuta*

5A. VULPIA MYUROS (L.) K. C. Gmelin var. MYUROS.—*Festuca myuros* L., Sp. Pl. 74. 1753. TYPE: “Habitat in Anglia (England), Italia”. —*Distomischus myuros* (L.) Dulac, Fl. Haut. Pyr. 91. 1867.—*Zerna myuros* (L.) Jacks., Ind. Kew 2:1249. 1895.—*Avena muralis* Salisb., Prodr. Stirp. 22. 1796. Based on *Festuca myuros* L.

DISTRIBUTION: Throughout the temperate-subtropical regions of the world. This is the most widely distributed *Vulpia*. It probably is native to central Europe but occurs as a common weed throughout southern

Europe, North and South Africa, the Orient, Australia, and North and South America. In Canada, the United States, and Mexico it is most frequent in coastal regions.

Vulpia myuros var. *myuros* appears closely related to *V. bromoides* from which it is distinguished primarily by the greatly reduced first glume. Hubbard (1968) reported a suspected hybrid between *V. myuros* var. *myuros* and *Festuca rubra* in the British Isles.

5B. VULPIA MYUROS (L.) K. C. Gmelin var. HIRSUTA Hack., Cat. Gram. Port. 24. 1880. TYPE: Portugal, "Coimbra". — *Festuca myuros* L. var. *hirsuta* (Hack.) Asch. & Graebn., Syn. Mitteleur. Fl. 2:588. 1901.

Festuca megalura Nutt., J. Acad. Nat. Sci. Philadelphia 2(1):188. TYPE: California, Santa Barbara, *Gambel s.n.* Location of type not known; Piper (1906) stated "... we have been unable to locate it in any American herbarium nor is it in the British Museum."—*Vulpia megalura* (Nutt.) Rydb., Bull. Torrey Bot. Club 26:538. 1909.

DISTRIBUTION: In many cool, temperate, and warm regions of the world including Europe, North and South America, the Hawaiian Islands, Japan, and Australia. In North America this taxon is most frequent along the west coast from central Alaska to Baja California. It is occasional throughout the Rocky Mountain area and Midwest and there are a few records from eastern states including Pennsylvania, South Carolina, Alabama, and Mississippi.

Plants of this taxon do not appear to be native to the United States as was assumed by Piper (1906), Hitchcock (1935), and others. *Vulpia myuros* var. *myuros* and *V. m.* var. *hirsuta* frequently grow intermingled in East Texas and herbarium collections often contain mixtures of the two varieties. Many California specimens of var. *hirsuta* are only sparsely ciliate on the lemma margins. Some European plants of var. *hirsuta* have lemmas that are much more conspicuously ciliate than those of North America plants and some reportedly have lemmas that are pubescent on the back as well as the margins. Plants grown at the Royal Botanic Gardens, Kew, England, from seed collected at the type locality, Coimbra, Portugal, were observed to have essentially the same lemma characteristics as the North American populations.

This treatment is based primarily on research of the first author (Lonard, 1970). We are indebted to the curators of the following herbaria for the loan of specimens during the course of this investigation: ARIZ, BM, CAS, GH, HSC, JEPS, K, LA, MICH, OKLA, SD, SMU, TAES, TEX, TTC, UC, US. Dr. Marion Ownbey has kindly supplied information concerning Suksdorf types in the herbarium of Washington State University. This is Technical Article No. 10514, Texas Agricultural Experiment Station, College Station, Texas 77843.

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VEGETATIONAL SUCCESSION ON COASTAL RANGELAND OF POINT REYES PENINSULA

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Most of Point Reyes Peninsula in Marin County, California, has recently become administered by the National Park Service to provide both public recreation and the continuance of some private livestock operations. Previous clearing of the land for pasture and continued cattle grazing have forced the coastal scrub and coastal prairie plant communities toward low seral stages of plant succession. Future recreational uses may eliminate cattle grazing and allow succession to advance toward a climax type. Our objective is to infer the composition of the early seres on abandoned rangeland by documenting the relative cover of the major plant species on three neighboring fields—one heavily grazed, one moderately grazed, and one protected from cattle grazing for the previous six years. The study plots have been permanently demarcated so comparative sampling in future years can document the presence of the climax type.

THE STUDY AREA

Point Reyes receives most of its precipitation during the late fall, winter, and spring. This Mediterranean type rainfall pattern, typical of much of California, is modified by the moisture condensed from summer fog. Climatic data for the Point Reyes Lighthouse are incomplete for the past 31 years; but the records correlate with those of San Francisco, 56 km to the southeast. San Francisco received 269 mm rainfall between July, 1971, and June, 1972. This was an unusually dry year. A 63 year average for the Point Reyes Lighthouse is 483 mm. However, the vegetational composition is predominately perennial and is not dramatically sensitive to annual variations in rainfall as confirmed by preliminary sampling in the previous normal year. The 60 year mean January temperature at the Lighthouse in 1941 was 9.8°C; mean July temperature was 12.1°C.

For nearly a century, Point Reyes Peninsula has been the site of grazing by dairy cattle (Mason, 1970). Visual reconnaissance of the topography and vegetative pattern, along with information gleaned from local ranchers, indicates that none of the area on the study plots had been cleared and planted for pasture, hay, artichokes, or peas as in some nearby fields. However, fires may have been set years ago in attempts to replace scrub with grassland. Early photographs by American Telephone and Telegraph Company of the heavily grazed field indicate that, approximately 45 years ago, it had clumps of perennial grass and scrub

similar to those presently found on the moderately grazed and protected fields.

The three study plots are within a radius of 0.8 km on level ground of the coastal plain immediately east of the dunes behind Point Reyes Beach (fig. 1). The plots vary in elevation from 24 m to 33 m on mesic soils of the Sheridan-Baywood association (Soil Conservation Service, 1967). This soil is deep, well-drained, sandy, and moderately acidic.

Plot I is a 37×92 m rectangle of heavily grazed grassland at the southern end of the enclosed field that surrounds the American Telephone and Telegraph radio station. Much of this 212 hectare field is covered by sand dunes and only 116 hectares are suitable for grazing (Jones, 1969). The heavy grazing results from a stocking rate of 1.16 forageable hectares per cow.

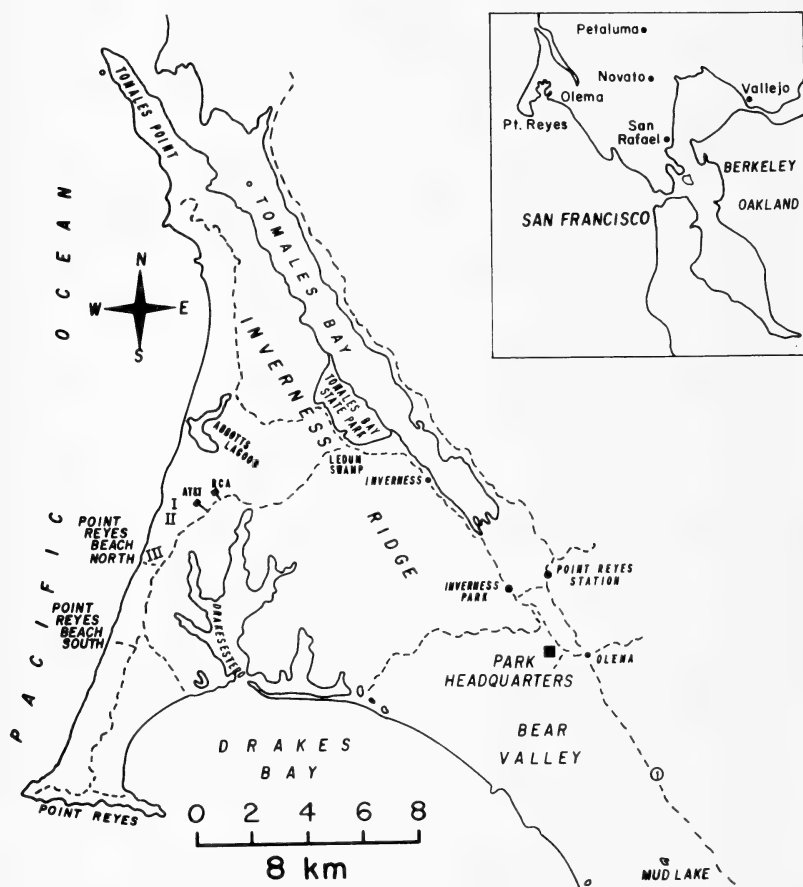


FIG. 1. Map of Point Reyes Peninsula, California, showing location of study area and study plots (I, II, and III).

Plot II is a 46×92 m "island" of mesic vegetation in the moderately grazed field. It is adjacent to plot I at the north end of the field just south of the A. T. & T. property. The grazing on this land has been moderate since at least 1949 at 2.63 hectares per cow.

Plot III is 18×82 m. It is the only substantial mesic patch in the ungrazed field. It is located immediately south of the moderately grazed field and had been exclosed for at least six growing seasons, since the National Park Service completed the northern access road to Point Reyes Beach in January, 1967.

METHODS

To facilitate comparisons between plots, we avoided both the xeric soils that supported sparse and stunted vegetation, and the hydric swales characterized by Howell (1970, p. 15) as supporting "rank growths of grasses, sedges, and rushes . . .". We restricted the plots to the mesic soil of "the drier mesa-like flats that are covered with low annuals and perennials".

To further substantiate the similarity of the plots, soil samples were collected by taking a core of the top 15 cm in each plot. They were weighed after air drying and root and litter material was separated by passing the soil through a 2 mm sieve. This organic fraction was expressed as a percentage of the initial soil weight. The moisture content of the recombined air dry soil was determined by difference after drying at 105°C for 48 hours. Soil pH, soil conductivity, and concentrations of water-soluble potassium, sodium, calcium, and magnesium were determined by methods described in Black et al. (1965). Although soils of the three plots differed somewhat (Table 1), the differences are not considered ecologically significant. For example, conductivities of 1.31, 1.47, and 2.17 millimhos all produce "mostly negligible" salinity effects according to the U. S. D. A. (Richards, 1954).

Vegetational sampling was done with the point-plot method (Heady, 1957). A frame holding ten vertical pins, as described by Heady and Rader (1958) was placed every 2.75 or 3.05 m along parallel transects 4.58 to 12.2 m apart to cover the varying sizes of the restricted plots.

TABLE 1. SUMMARY OF SOIL ANALYSIS.

Test	Plots		
	I	II	III
Moisture loss of air dry soil when heated to 105°C	1.23%	1.61%	1.54%
Amount of organic matter (roots and litter)	0.52%	3.74%	1.42%
Water soluble			
K	0.184	0.272	0.522
Na	1.52	2.14	5.64
Ca	0.935	1.42	1.89
Mg	1.09	1.60	2.93
(expressed in milliequivalents/100 gm oven-dry soil)			
Conductivity (millimhos)	1.31	1.47	2.17

Each pin was pushed downward and the first species hit along with the height above the ground of the pin's contact were recorded. The total number of hits on a species, calculated as a percentage of the total number of hits on all species, determined the relative cover value of that species. Any hit on unattached vegetation was defined as litter.

Plot III was sampled during the last week of April, 1972, and plots I and II were sampled together during a month beginning the last week of May, 1972. Variation of relative cover due to growth within the month interval between samplings was small because of the predominantly perennial type vegetation. The only important species noted to become senescent at the later sampling was *Ranunculus californicus*.

Approximately 1,400, 1,500, and 1,550 points were sampled on Plots I, II, and III, respectively. To determine the variability of the sampling technique, relative cover values on all plots were calculated at 100-point intervals for species whose final values were greater than 4 percent. For intervals above 1,000 points, the average of the deviations for all such species was 12 percent of the final percentages, and above 1,300 points, the average was 6 percent.

Chi-square values were used to determine significant differences of relative cover between plots. They were calculated with a standard two by-two contingency table and corresponding equation as given by Knight (1965). Only species of 0.5 percent or greater relative cover, before being rounded to the nearest 0.5 percent, are discussed below. Many species of lower relative cover values were present, but chi-square values determined that a relative cover below 0.5 percent was not significantly different from 0.0 percent. Voucher specimens, identified according to Munz (1959, 1968), have been deposited in the herbarium of Point Reyes National Seashore, Point Reyes, California 94956.

RESULTS AND DISCUSSION

The average heights per pin for all pins hitting vegetation on plots I, II, and III were 5.0, 11.0, and 16.5 cm, respectively. These average heights substantiate well the different visual appearances of the three plots. The gradation of heights is a function of both differential grazing pressure by cattle and species composition.

Table 2 lists the relative cover values for the species on each plot in order of decreasing values on plot III. Successional changes are inferred from significant differences between plots that represent different seres.

The heavily grazed field, plot I, is dominated by species adapted to withstand grazing. *Eryngium armatum* is a low, prostrate forb with stiff, prickly spines. *Baccharis pilularis* ssp. *pilularis* is a shrub that is considered unpalatable to livestock (McBride and Heady, 1968), although it is browsed in heavily grazed pastures on neighboring dairy ranches. *Danthonia californica*, a native perennial grass, has protected cleistogamous florets and a low spreading form. The exotic annuals, *Aira*

Table 2. RELATIVE COVER ON COASTAL RANGELAND PLOTS SUBJECTED TO DIFFERENTIAL GRAZING PRESSURE. Successional changes are inferred from significant differences between plots ($P < 0.05$) indicated by asterisks between adjacent columns. Values are percentages of total vegetative hits per plot. "hit" indicates the species was hit less than 0.5 percent; — indicates no hits; NP = Native Perennial; NBi = Native Biennial; IP = Introduced Perennial; IA = Introduced Annual; # = indicator species of coastal prairie; † = indicator species of coastal scrub.

Taxon	Origin and seasonality	Relative cover on plots (%)		
		I	II	III
# <i>Deschampsia caespitosa</i> ssp. <i>holciformis</i>	NP	3.5 *	15.5 *	23.0
† <i>Baccharis pilularis</i> ssp. <i>pilularis</i>	NP	13.5 *	18.0 *	12.0
<i>Bromus carinatus</i>	NBi	2.0	2.5 *	9.5
<i>Rumex Acetosella</i>	IP	3.5	2.0 *	6.0
# <i>Pteridium aquilinum</i> var. <i>pubescens</i>	NP	3.0 *	4.0	4.5
<i>Hordeum brachyantherum</i>	NP	0.5 *	5.0	3.5
<i>Lolium perenne</i>	IP	4.5 *	6.5 *	3.0
<i>Achillea borealis</i> ssp. <i>californica</i>	NP	2.5	2.5	3.0
<i>Plantago lanceolata</i>	IP	3.0 *	9.0 *	3.0
# <i>Iris Douglasiana</i>	NP	hit *	1.5	3.0
# <i>Ranunculus californicus</i>	NP	—	— *	3.0
# <i>Holcus lanatus</i>	IP	— *	2.0	2.5
<i>Armeria maritima</i>	NP	—	— *	2.5
<i>Elymus glaucus</i>	NP	1.0	1.0 *	2.0
<i>Rhus diversiloba</i>	NP	—	— *	2.0
# <i>Sisyrinchium bellum</i>	NP	1.5	1.0	2.0
† <i>Rubus vitifolius</i>	NP	hit	hit *	1.5
<i>Cirsium quercetorum</i>	NP	2.0 *	0.5 *	1.5
<i>Stachys rigidus</i> ssp. <i>quercetorum</i>	NP	hit	hit *	1.0
# <i>Danthonia californica</i>	NP	7.0 *	3.5 *	1.0
<i>Festuca dertonensis</i>	IA	5.5	4.5 *	1.0
<i>Hypochoeris radicata</i>	IP	5.5	4.5 *	1.0
<i>Chlorogalum pomeridianum</i>	NP	—	— *	1.0
<i>Grindelia stricta</i> ssp. <i>venulosa</i>	NP	—	— *	0.5
<i>Bromus mollis</i>	IA	hit *	1.0	0.5
<i>Perideridia Kelloggii</i>	NP	—	hit *	0.5
# <i>Carex tumulicola</i>	NP	1.0	1.0	0.5
<i>Vicia americana</i> var. <i>linearis</i>	NP	—	— *	0.5
<i>Phleum alpinum</i>	NP	hit	— *	0.5
† # <i>Lupinus variicolor</i>	NP	1.0 *	3.0 *	hit
<i>Juncus Lesueurii</i>	NP	0.5	0.5	hit
<i>Juncus phaeocephalus</i>	NP	4.0 *	1.5 *	hit
<i>Aira caryophyllaea</i>	IA	8.0 *	4.5 *	hit
<i>Briza minor</i>	IA	0.5	hit	hit
<i>Galium Aparine</i>	IA	—	0.5	hit
<i>Horkelia marinensis</i>	NP	1.0	hit	hit
<i>Cardionema ramossissimum</i>	NP	2.0 *	0.5 *	—
<i>Eryngium armatum</i>	NP	17.0 *	1.0 *	—
<i>Hypochoeris glabra</i>	IA	1.0	hit	—
<i>Agrostis</i> spp.	NP	1.0 *	—	—
<i>Panicum pacificum</i>	NP	1.0 *	—	—

caryophyllea and *Festuca dertonensis*, are small grasses and are the first to set seed. Thus, they have a higher probability of leaving seeds for the following year than do taller, slower growing perennials. Heavy grazing also results in more open ground where annual species can successfully germinate.

Indicative of the moderate grazing on plot II are the high relative covers of the palatable species *Plantago lanceolata* and *Lolium perenne*. This grazing pressure permitted *Baccharis pilularis* ssp. *pilularis*, a low shrub, to reach its highest relative cover and co-dominate plot II with *Deschampsia caespitosa* ssp. *holciformis*, a native bunch grass.

The mesic area of the protected field, plot III, can be described as predominantly a perennial grassland with clumps of low scrub. Nine species present are indicator species for the coastal prairie plant community (Munz, 1959) and three are indicator species for the northern coastal scrub community (Table 2), which is described as "... often with extensive areas of grass (*Danthonia californica*, *Deschampsia caespitosa* ssp. *holciformis*, *Calamagrostis nutkaensis*, *Holcus lanatus*, etc.) ..."

The total relative covers of perennial and biennial species on plots I, II, and III were 81.5, 87.5, and 94.0 percent, respectively. Chi-square values determined significant differences between them ($P < 0.5$). This substantiates the following:

1) Climatic and edaphic factors influencing the study areas favor perennial plants. Summer fog extends the wet season and allows perennial species to thrive (Davy, 1902) and to dominate the xeric-adapted annuals. Inferiority of annuals in this environment is emphasized by the relative rarity of annual wild oats (*Avena* spp.) on the peninsula, although they were once cultivated there for hay, have spread successfully throughout much of California (Robbins et al, 1951), and are abundant directly inland on the eastern side of Tomales Bay.

2) Grazing pressure has created a disclimax on plots I and II as compared with the protected community of plot III. Although some native California plants are believed to contain volatile chemicals that deter native ungulate grazing (Longhurst et al., 1968), they remain palatable to domestic livestock. Thus, they are subject to heavy use, which reduces plant vigor and removes a critical amount of mulch. This causes an increase in species characteristic of lower seral stages (Heady, 1966), i.e., the increase of exotic annual species and a decrease in the native (predominantly perennial) vegetation on the heavily and moderately grazed plots (Table 3).

3) The removal of cattle from plot III has caused a successional change toward a climax community in the last six growing seasons. It is now composed of 78.5 percent native species compared with 65.0 percent on the heavily grazed plot. However, it may never recover pristine climax conditions. The perennials *Rumex Acetosella*, *Lolium perenne*,

TABLE 3. TOTAL RELATIVE COVERS ON PLOTS. Asterisks between adjacent columns indicate significant differences ($P < 0.05$) between plots.

	Relative cover on plots (%)					
	I		II		III	
Perennial and biennial species	81.5	*	87.5	*	94.0	
Annual species	15.0		10.5	*	1.5	
Native species	65.0	*	63.5	*	78.5	
Introduced species	31.5	*	34.5	*	17.0	
Species less than 0.5%	3.5		2.0		4.5	

Plantago lanceolata, *Holcus lanatus*, and *Hypochoeris radicata*, with total relative cover of 15.5 percent, are exotic species that are so well adapted to the environment that they can be expected to be retained as a part of the climax community (H. F. Heady, personal communication). Also, tule elk, which once foraged on the peninsula and were seen with "a thousand elk in one herd" (Mason, 1970, p. 19), may have had an effect on the composition of the vegetation. And the frequency of fire may have changed. Fire may have periodically swept through the area modifying the grassland to fire-resistant species, and reducing the scrubland to grassland (Wells, 1962).

Only surveys repeated in future years will determine whether climatic, edaphic, and zootic climaxes are currently present on the field protected from cattle grazing.

ACKNOWLEDGMENTS

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NOTES AND NEWS

A RANGE AND ELEVATION EXTENSION FOR *IPOMOPSIS POLYCLADON*.—On 5 May 1973 I discovered a small population of *Ipomopsis polycladon* (Torr.) V. Grant on southwest-facing slopes of gravelly soil at about 1140 m in Upper Johnson Valley, T6N, R3E, Sec. 25, San Bernardino County, California (voucher: UCR 13396). *Ipomopsis polycladon* has been described as rare in California (Munz, P.A., *Manual of Southern California botany*, The Lancaster Press, Inc., Lancaster, Pa., 1935) in the eastern Mohave Desert, notably near Needles and from the Argus, Ivanpah, and Kingsten ranges. A review of the literature and of the few specimens at JEPS, RSA, and UC revealed two unpublished elevation and two unpublished range extensions. The elevation extensions derive from a specimen collected by P. A. Munz at 2044 m near Bridgeport, Mono County, and one by V. Duran at 2135 m in the White Mountains (UC 809749 and 908125), both above the 1610 m maximum given by Munz (*A California flora*, University of California Press, Berkeley, 1959). Range extensions include a find by G. T. Robbins et al. near Hector Mine, 3 km south of Pisgah (JEPS 8002), one collection, 6 km northwest of Adelanto, by J. and L. Roos, near Red Raven Mine (RSA 92547), and now the Upper Johnson Valley collection, all in western San Bernardino County. The range extensions are about 160 km south from the Argus and Kingston ranges, and from about 175 to 275 km west from the eastern desert localities at the Ivanpah range and Needles. The Johnson Valley find may be important because California specimens number less than thirty, none have been collected since 1958, and because a power generating station is planned on the site of collection.—DAVID H. ESLINGER, Dry Lands Research Institute, University of California, Riverside 92502.

SYSTEMATICS OF *CIRSIMUM* (COMPOSITAE) IN WYOMING

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Ohio State University)

Wyoming thistles (*Cirsium* spp.) are found in a wide range of habitats, from mesic to arid and lowland (1110 m) to alpine (3450 m). Many are particularly suited to invasion of disturbed sites and are common roadside weeds throughout much of the state.

Taxonomists have differed as to the number of native species of *Cirsium* in Wyoming, from as few as eight to as many as 21 (Rydberg, 1906, 1917; Coulter and Nelson, 1909; Petrak, 1917). More recently, Frankton and Moore (1961) and Moore and Frankton (1963, 1964, 1965, 1967, and 1969), using cytological as well as morphological data to delimit taxa, suggest that 16 *Cirsium* species probably occur in the state.

In attempting to understand the genus, I have employed morphological studies, field observations, chromosome numbers, and leaf flavonoid chemistry. Although this treatment is limited to the species of *Cirsium* that occur in Wyoming, field work was carried out in adjacent states. In addition, specimens of foliose thistles from Canada and the western United States, all annotated by R. J. Moore, were borrowed from the Canadian Department of Agriculture, Ottawa, Canada (DAO). All specimens cited in this paper are deposited in the Rocky Mountain Herbarium (RM) unless otherwise indicated.

MATERIALS AND METHODS

Standard techniques were used in determining chromosome numbers (Gardner, 1972). For seed germination the procedures of Ownbey and Hsi (1963) were followed, and root tip staining was achieved by Snow's (1963) method. Voucher specimens for all counts are deposited in RM.

Paper chromatography was employed on a minimum of five collections from different populations, following the procedures of Crawford (1970). Thin layer chromatography was used to characterize flavonoid profiles of additional specimens. Certain species were characterized by high chlorophyll and lipid concentrations and relatively low flavonoid content, and it was necessary to pre-extract with ether in order to remove these excess compounds. After determining color reactions and R_f values on paper chromatograms, and ultraviolet spectroscopy of the purified compounds, the phenolics were identified by comparing their properties with published results (ApSimon et al., 1963; Doherty et al., 1963;

Harborne, 1967; Challice and Williams, 1968; Mabry et al., 1970; Wallace and Bohm, 1971; Giannasi, 1972; Mears and Mabry, 1972). When sufficient material was available, individual compounds were hydrolyzed. Both acidic and enzymic hydrolyses were attempted, using the procedures outlined by Harborne (1965).

CYTOLOGY

In this study, ten species of *Cirsium* were found to have $2n = 34$ (Table 1), suggesting a base number of $x = 17$. Three taxa, i.e., *C. flodmanii*, $2n = 22$; *C. undulatum*, $2n = 26$; and *C. ochrocentrum*, $2n = 30$ and 32 , have numbers that are considered reductions (cf. Frankton and Moore, 1961). Variation was found in single collections of *C. coloradense*, $2n = 32$ (fig. 1) and *C. centaureae*, $2n = 36$ (fig. 1). However, other collections of these species have the usual $2n = 34$. With these exceptions, my counts agree with published reports. Cytological data are included under the discussion of *Cirsium pulcherrimum* and *C. subniveum* because of their importance in differentiating the two taxa.

LEAF FLAVONOID STUDIES

Flavonoid studies were made on the leaves of 11 Wyoming species of *Cirsium*. Although the taxa studied produce similar leaf flavonoids, none has a profile identical to another (fig. 2). These chemical features have been extremely useful from a taxonomic standpoint, particularly with those species that are morphologically similar.

Of the 19 flavonoids identified (Table 2), ten are methylated flavone glycosides, i.e., acacetin, diosmetin, and chrysoeriol. In addition to B-

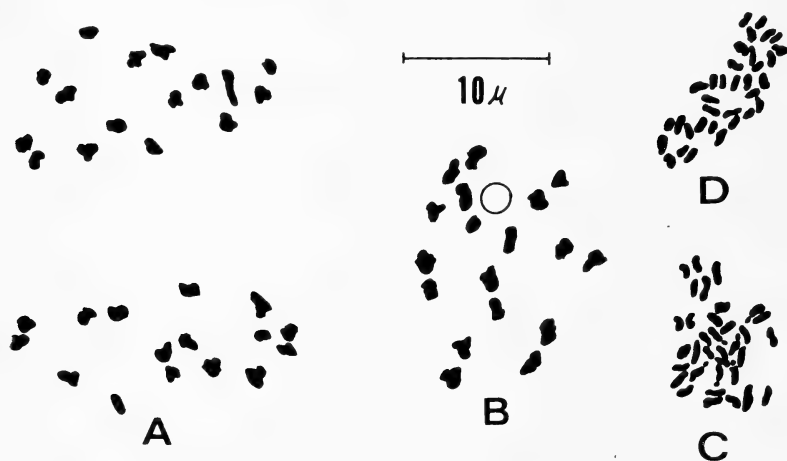


FIG. 1. Camera lucida drawings of *Cirsium* chromosomes. A. *C. coloradense*, first telophase ($n = 16$); B. *C. centaureae*, diakinesis ($n = 18$); C. *C. subniveum*, mitotic metaphase ($2n = 34$); D. *C. pulcherrimum*, mitotic metaphase ($2n = 34$).

TABLE 1. CHROMOSOME NUMBERS IN SOME SPECIES OF CIRSIUM. Collection numbers are those of the author and voucher specimens are in RM. Collections marked with an asterisk (*) are illustrated in Figure 1.

Cirsium canescens Nutt. $n = 17$. Colorado: Larimer Co.: Albany County Road 34 to Colorado, 27 mi SW of Laramie, Wyoming, 159; Wyoming: Albany Co.: 2 mi SE of Laramie, 108, 109, 110; Hwy. 34, $\frac{1}{2}$ mi E of Morton's Pass, 117; Laramie Co.: I-80, 7 mi W of Cheyenne, 156A; Hwy. 214, 1 mi S of I-80 Burns-Carpenter Exit, 168.

Cirsium centaureae (Rydb.) K. Schum. $n = 17$. Colorado: Larimer Co.: Hwy. 34, 6 mi E of Estes Park, 116; Wyoming: Albany Co.: NE of Laramie, 1 mi SE of quarry, 143. $n = 18$. Hwy. 130, 3 mi W of Centennial, 146*.

Cirsium coloradense (Rydb.) Cockerell. $n = 17$. Colorado: Larimer Co.: Albany County Road 34 to Colorado, 29 mi SW of Laramie, Wyoming, 161; 32 mi SW of Laramie, Wyoming, 162B; Wyoming: Albany Co.: County Road, 3 mi N of Fox Park, 166. $n = 16$. Hwy. 287, 9 mi S of Laramie, 111*; Carbon Co.: Road to Shirley Basin, 14 mi from intersection of Hwy. 487, 125. $n = 17$. Hwy. 130, 3 mi W of Ryan Park, 147A.

Cirsium drummondii Torrey & Gray, $2n = 34$. South Dakota: Custer Co.: Hwy. 87, 1 mi NE of west entrance to Custer State Park, 174.

Cirsium flodmanii (Rydb.) Arthur. $n = 11$. Colorado: Weld Co.: road between Hereford and Grover, 1 mi S of Hereford, 169; South Dakota: Custer Co.: all along road through Custer State Park, 173; Wyoming: Johnson Co.: Hwy. 16, 3 mi NE of Buffalo, 136; Hwy. 87, 23 mi. S of Buffalo, 186; Weston Co.: Old Boyd Townsite, E. of Four Corners Store, 176.

Cirsium foliosum (Hook.) DC. $2n = 34$. Wyoming: Sheridan Co.: Hwy. 14 alternate, 4 mi W of Burgess Jct., 191.

Cirsium ochrocentrum A. Gray. $n = 16$. Wyoming: Fremont Co.: Hwy. 26-287, 17 mi NW of Lander, 209; Laramie Co.: I-80, 10 mi E of Cheyenne, 167. $n = 15$. I-25, 15 mi S of Chugwater, 155; Platte Co.: Hwy. 126, 12 mi E of jct. with I-25, 121. $n = 16$. Hwy. 34, $\frac{1}{2}$ mi SW of Sybille Creek, 154.

Cirsium pulcherrimum (Rydb.) K. Schum. $n = 17$. Wyoming: Washakie Co.: Hwy. 16, 30 mi E of Tensleep, 131, 132; Sweetwater Co.: 5 mi S of Creston Jct., 153. $2n = 34$. Road to Bitter Creek, 6 mi S of I-80, 211*.

Cirsium scariosum Nutt. $n = 17$. Wyoming: Yellowstone National Park: east entrance road, 18 mi W of entrance, 196.

Cirsium subniveum Rydb. $2n = 34$. Wyoming: Grand Teton National Park: Gros Ventre Campground, 199*; Teton Co.: along roadside at jct. of Hoback and Snake Rivers, 200.

Cirsium undulatum (Nutt.) Spreng. $n = 13$. Colorado: Larimer Co.: Hwy. 287, 15 mi N of Fort Collins, 113; Wyoming: Albany Co.: Hwy. 34, 6 mi E of Morton's Pass, 118; Goshen Co.: Hwy. 85, 15 mi S of Torrington, 178; Washakie Co.: Hwy. 16, 25 mi E of Tensleep, 130.

Putative hybrids:

Cirsium coloradense \times *C. canescens*. $n = 16$. Colorado: Larimer Co.: Albany County Road 34 to Colorado, ca. 25 mi SW of Laramie, Wyoming, 158A. $n = 17$. 158C; Wyoming: Albany Co.: County Road 17, 1 mi NW of Horse Creek, 142; Carbon Co.: Hwy. 130, 3 mi W of Ryan Park, 147C.

Cirsium tweedyi \times *C. pulcherrimum*. $2n = 35$ & 36. Wyoming: Sheridan Co.: Hwy. 14, 15 mi E of Burgess Jct., 189.

ring methylation, 6-methylated apigenin, acacetin, and chrysoeriol have been found. Although few reports of methylated compounds from the leaves of *Cirsium* exist in the literature (Harborne, 1967; Wallace and

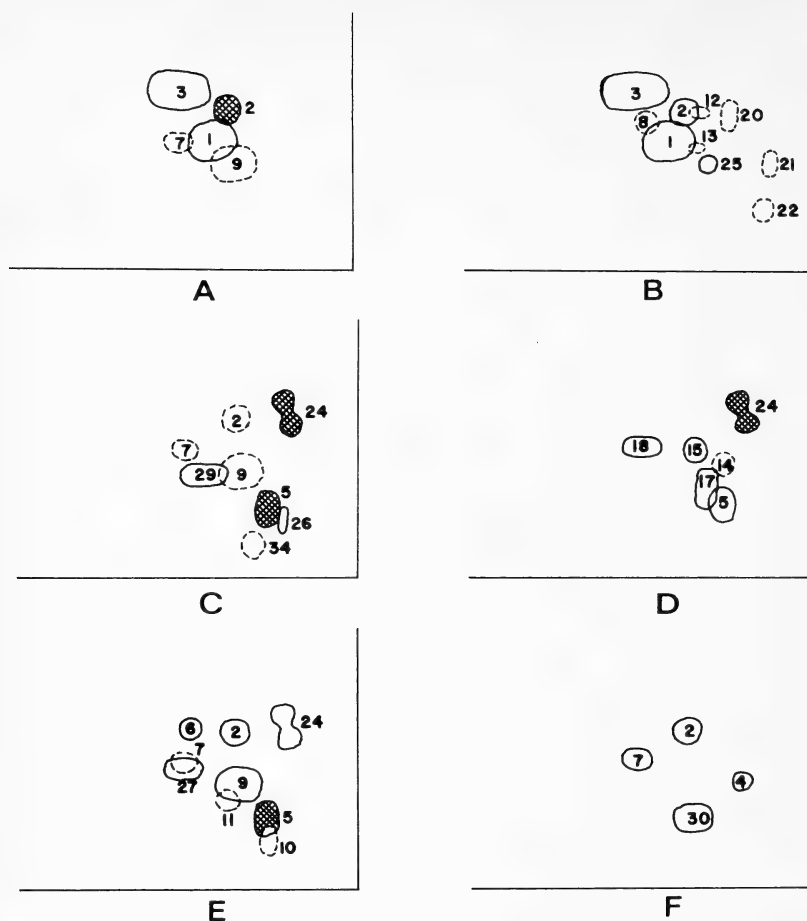


FIG. 2. Drawings of 2-dimensional paper chromatograms of *Cirsium* leaf extracts. Cross-hatching indicates compounds common to both taxa being considered. A. *C. coloradense*, solid line; *C. scariosum*, dashed line; B. *C. foliosum*, solid line; *C. drummondii*, dashed line; C. *C. flodmanii*, solid line; *C. undulatum*, dashed line; D. *C. canescens*, solid line; *C. ochrocentrum*, dashed line; E. *C. subniveum*, solid line; *C. pulcherrimum*, dashed line; F. *C. tweedyi*.

Bohm, 1971; McGowan and Wallace, 1972; Moriata et al., 1973), methylation is characteristic of the Wyoming species of the genus. Five 7-O-glycosides of the common flavones apigenin, luteolin, and vicenin, the 6-, 8-di-*C*-glycoside of apigenin, were also found. An additional eight unidentified compounds (Table 3) were considered to be of taxonomic value.

HYBRIDIZATION

There are numerous reports of *Cirsium* hybrids in the literature (Rydberg, 1917; Petrak, 1917; Cronquist, 1955; and Moore and Frank-

TABLE 2. IDENTIFIED LEAF FLAVONOIDS OF WYOMING CIRSIIUM. Spot designations correspond to those in Figure 2.

Spot-designation	Identity of Flavonoid
1	acacetin 7- <i>O</i> -rutinoside
2	quercetin 3- <i>O</i> -diglycoside
3	6-methoxy acacetin 7- <i>O</i> -rutinoside #
5	chrysoeriol 7- <i>O</i> -diglycoside
6	quercetin 3- <i>O</i> -diglycoside
7	quercetin 3- <i>O</i> -diglycoside
9	diosmetin 7- <i>O</i> -diglycoside *
10	luteolin 7- <i>O</i> -diglycoside
11	apigenin 7- <i>O</i> -di?glycoside
14	diosmetin 7- <i>O</i> -di?glycoside? *
15	6-methoxy apigenin 7- <i>O</i> -diglucoside *
17	6-methoxy chrysoeriol 7- <i>O</i> -diglucoside*
18	apigenin 7- <i>O</i> -diglucoside
20	6-methoxy apigenin 8- <i>C</i> -glycoside?
24	apigenin 6-, 8- <i>C</i> -diglycoside
27	acacetin 7- <i>O</i> -diglycoside
29	apigenin 7- <i>O</i> -diglycoside
30	luteolin 7- <i>O</i> -diglycoside?
34	chrysoeriol 7- <i>O</i> -monoglycoside

otherwise known only from Japanese and European members of the genus (Harborne, 1967).

* first report of this compound from *Cirsium*.

TABLE 3. UNIDENTIFIED LEAF COMPOUNDS OF WYOMING CIRSIIUM. Spot designations correspond to those in Figure 2.

Spot designation	Color reactions on paper chromatograms*		R _f Values	
	UV	UV+NH ₃	TBA	HOAc
4	D	D	.41	.51
8	D	G	.47	.59
12	D	G	.34	.62
13	D	D	.32	.49
21	D	G	.11	.42
22	D	D	.12	.24
25	D	D	.29	.42
26	D	Y	.21	.22

* D = dark (no change), Y = yellow, G = green.

ton, 1967). Most of the hybrids listed involve either *C. coloradense* (Rydb.) Cockerell or *C. tioganum* (Congd.) Petrak as one of the parents.

During the course of my field work, I collected 21 plants that are apparent hybrids. Of these, I believe that 20 involve *Cirsium coloradense* as one parent. In some of the collections, leaf flavonoid profiles support the morphological data in the interpretation of these plants as hybrids, whereas in others, only the compounds of one putative parent were found and morphology is the only evidence for hybridization. The majority of putative hybrids that I found were in south central Wyoming

and adjacent Colorado. Generally, several hybrid plants occur in the same locality, suggesting that when isolating mechanisms break down, the plants hybridize freely.

The additive nature of flavonoid compounds has been shown to be quite useful as an additional character for documenting hybridization (Turner and Alston, 1959; Alston and Turner, 1962), but in the present study of hybrids, only five of the 21 putative hybrids display an additive chemical profile. All hybrids involving *C. coloradense* contain the compounds characteristic of that species, whereas only five of these plants produced any flavonoids normally found in the other putative parents i.e., *C. canescens* or *C. pulcherrimum*. It is possible that most of the specimens found are backcrosses to *C. coloradense* and that, as shown by Levin (1967), the profile of the non-recurrent parent can be lost in a first or subsequent generation backcross. It is also possible that the collections are advanced generation hybrids, and, if the loci governing the production of a given series of compounds are linked, these features could be lost through segregation (Belzer and Ownbey, 1971). Finally, the apparent lack of compounds typical of *C. canescens* or *C. pulcherrimum* may be quantitative rather than qualitative as a result of poor penetrance (Belzer and Ownbey, 1971). The acacetins produced by *C. coloradense* are much more concentrated than the flavonoids found in the profiles of *C. canescens* or *C. pulcherrimum*. It is significant that in the hybrids that do show a partially additive profile, the acacetins of *C. coloradense* appear to be of normal intensity, while the compounds of the other putative parents are somewhat reduced in quantity as compared to a "pure" *C. canescens* or *C. pulcherrimum* profile.

KEY TO THE SPECIES OF CIRSIMUM IN WYOMING

1. Involucre of largest mature heads (0.9–) 1.2–1.7 (–2.0) cm tall, 0.6–1.0 cm broad at the base; heads numerous, in loose corymbiform clusters; heads of two kinds, if pappus longer than corolla, anthers 1–2 mm long, if pappus shorter than corolla, anthers 4–5 mm long 14. *C. arvense*
1. Involucre of largest mature heads more than 1.8 cm tall, 1 cm or more broad at base; heads solitary or in compact terminal clusters or axillary, not in corymbiform clusters; all anthers of similar length 2.
2. Involucre of mature heads 3.5–5.0 cm tall; margins of inner rows of phyllaries dilated and lacerate near tip, usually with a glutinous dorsal ridge; yellow apical collar on achenes 0.4–0.8 mm broad 3. *C. drummondii*
2. Plants not having the same combinations as above 3.
3. Heads frequently in terminal clusters, occasionally axillary on upper half of stem; all heads exceeded by one to several cauline leaves; leaves not markedly reduced upwards; phyllaries without a glutinous dorsal ridge (occasionally a few glands on *C. tweedyi*) 4.
3. Heads borne singly or in loose clusters, always one terminal on stem and branches, occasionally axillary on upper half of stem; heads never appreciably exceeded by cauline leaves; leaves markedly reduced upwards; phyllaries with or without a glutinous dorsal ridge 7.
4. Pappus longer than the corolla by 1 mm or more; achenes 4 mm long and 2 mm or less broad 4. *C. foliosum*

4. Pappus shorter than the corolla; achenes longer than 4 mm and 2 mm or more broad 5.
 5. Leaf bases of most cauline leaves decurrent, wings 6–30 mm long; leaves glabrous above and below, rarely a thin tomentum below; involucre 1.0–1.5 cm broad at base 11. *C. tweedyi*
 5. Leaf bases of all leaves clasping, not decurrent; leaves tomentose below; involucre 1.5–3.0 cm broad at base 6.
 6. Sinus depth 75% or more of leaf width, when the middle portion of lower leaves is measured; pappus 22–24 mm long; corolla 22–29 mm long; style 26–32 mm long 1. *C. coloradense*
 6. Sinus depth 74% or less of leaf width, when measured as above; pappus 14–21 mm long; corolla 16–24 mm long; style 19–26 mm long 2. *C. scariosum*
 7. Phyllaries with coarsely lacerate margins, dilated in upper half; without a glutinous dorsal ridge 12. *C. centaureae*
 7. Phyllaries with subtentire or entire margins, tapering in upper half; usually with a glutinous dorsal ridge 8.
 8. Upper leaf surfaces with minute, appressed spines, otherwise glabrous; outer phyllaries to 1 mm broad at base and reflexed near middle 13. *C. vulgare*
 8. Upper leaf surfaces without appressed spines, either glabrous or tomentose; outer phyllaries 1–3 mm broad at base, not reflexed, although spines may be reflexed at base 9.
 9. Leaves clasping stem, rarely decurrent, if so, wings less than 12 mm long 10.
 9. Leaves decurrent, wings of middle cauline leaves at least 15 mm long. 11.
 10. Yellow apical collar on achenes 0.4–0.7 mm broad; rosette leaves, at least a few, and occasionally all cauline leaves entire, with marginal spines; upper leaf surface usually green 6. *C. flodmanii*
 10. Yellow apical collar on achenes to 0.2 mm broad or lacking; rosette leaves and cauline leaves dissected, rarely subtentire; upper leaf surface usually gray 5. *C. undulatum*
 11. Decurrence of lowermost leaves greater than that of uppermost leaves; phyllaries conspicuously arachnoid pubescent, the hairs extending from margin of one phyllary to margin of adjacent phyllary 10. *C. subniveum*
 11. Decurrence of lowermost leaves less than or nearly equal to that of uppermost leaves; phyllaries, if pubescent at all, only sparsely so along margins, rarely extending from phyllary to phyllary 12.
 12. Lower leaves with at least some lobes 3.5–5.5 times longer than broad; involucre essentially square, phyllary spines 4 mm or less long, rarely to 5 mm long 8. *C. canescens*
 12. Lower leaves without any lobes as much as 3 times longer than broad (rarely longer in *C. pulcherrimum*, but then upper leaf surface is bright green); involucre taller than broad; phyllary spines 4 mm or more long 13.
 13. Involucre of mature heads 1.8–2.7 cm tall; upper leaf surface usually glabrous, rarely lightly tomentose 9. *C. pulcherrimum*
 13. Involucre of mature heads 3.0–3.5 cm tall; upper leaf surface lightly tomentose to densely so 7. *C. ochrocentrum*
1. *CIRSIUM COLORADENSE* (Rydb.) Cockerell ex Daniels, Univ. Missouri Studies, Sci. Ser. 2(2):402. (Oct) 1911.—*Carduus coloradense* Rydb., Bull. Torrey Bot. Club 32:132. 1905. TYPE: Colorado: Pagosa Springs, 1899, *C. F. Baker* 644. (Holotype: NY, not seen; Isotype: POM, not seen).

Plants acaulescent or with stems 3–6 (–8) dm tall; stems simple, rarely the upper portions with slender branches to 1 dm long; heads subtended by one to several leaves (lower leaves 18–30 cm long, 3–5 cm wide, sinus depth 75–90% of leaf width, subtending leaves 5–14 cm long, 1–3 cm wide, subtire to 100% divided), leaf bases clasping, marginal spines 5–15 mm long, generally longest on subtending leaves; heads axillary, scattered, sessile or on short peduncles (to 3 cm long), involucre 2–3 cm tall, 1.5–3.0 cm broad, about as broad as tall, with (5–) 7–10 (–12) rows of phyllaries, non-glandular, sometimes with dark midline; pappus (17–) 22–24 mm long; corolla white to pink, 22–29 mm long, the lobes 4–6 (–7) mm long; anthers 8–10 mm long; style 26–32 mm long, the branches 4–6 mm long; achenes 5–6 mm long, 2–3 mm wide, with or without a narrow yellow apical collar; flowers in mid-July and mature achenes are produced throughout August.

DISTRIBUTION: S Wyoming to Arizona and New Mexico. In Wyoming (fig. 3), it is often a weed of roadsides, pastures, or fields, usually in depressions or along drainages, suggesting a preference for moist sites; 1320–2450 m.

REPRESENTATIVE SPECIMENS: Wyoming: Albany Co.: Laramie, near High School, 3 Aug 1961, *Porter & Porter 8819*; Cummins, E side of

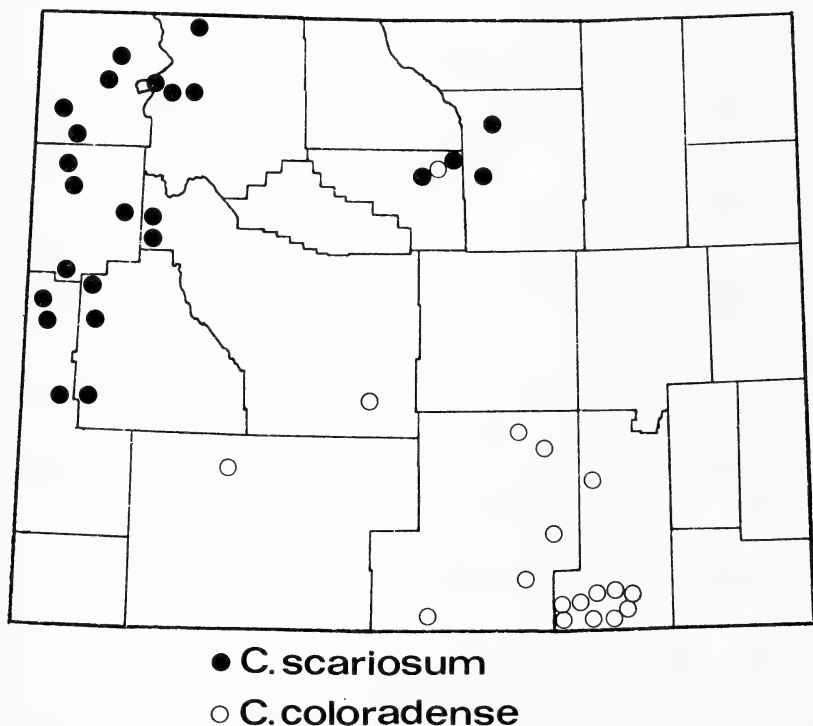


FIG. 3. Documented Wyoming distribution of *C. scariosum* and *C. coloradense*.

bridge, 6 Aug 1971, *Gardner 180A* (stemmed), *180B* (acaulescent). Carbon Co.: 14 mi N of Hwy. 487, road to Shirley Basin, 6 Jul 1971, *Gardner 125*; Hwy. 70, 30 mi E of Baggs, near Savory Stock Drive, 22 Jul 1971, *Gardner 151A* (5 dm tall), *151B* (2.2 dm tall). Fremont Co.: Hwy. 287-789, 10 mi W of Jeffrey City, 12 Aug 1971, *Gardner 210*. Sweetwater Co.: road to Boar's Tusk, 17 Aug 1971, *Gardner 212*. Washakie Co.: Hwy. 16, 1 mi E of Tensleep, 7 Jul 1971, *Gardner 129*.

In Wyoming, *Cirsium coloradense* often is confused with the closely related *C. scariosum* of the northwestern part of the state. A third closely related species, *C. tioganum* (Congd.) Petrak, has also been reported from the area. According to Moore and Frankton (1967), the latter taxon is characterized by being acaulescent (rarely stemmed), with oblanceolate leaves tapering basally to little more than a broad midvein. The author has not found any *Cirsium*, in the field nor in herbaria, with consistently oblanceolate leaves. Basal tapering of leaves is characteristic of most collections of all foliose thistles. I do not recognize these characteristics as sufficient to delimit the species and therefore, exclude *Cirsium tioganum* from the flora of Wyoming. A few specimens from Nevada and California fit the descriptions of the taxon more closely, but additional study is needed to determine if *C. tioganum* is in fact a "good" species.

All Wyoming acaulescent *Cirsium* that I have seen are *C. coloradense*. Two short stemmed plants (both about 5 cm tall) fall within the range of *C. scariosum*. These two species are most easily separated on corolla length and sinus depth/leaf width (fig. 4). It should be noted that plants with stems 1 dm or less tall are in both morphological ranges.

2. *CIRSIUM SCARIOSUM* Nutt., Trans. Amer. Philos. Soc. 7:420. 1841. TYPE: Idaho: Bingham Co.: Fort Hall, "Prairies of the Rocky Mts.", 1834, *Nuttall s.n.* (Holotype: BM, not seen).—*Cnicus scariosus* (Nutt.) A. Gray, Syn. Flora North Amer. 1:402. 1897.—*Carduus scariosus* (Nutt.) Heller, Cat. North Amer. Plants 7:134. 1898.

Carduus kelseyi Rydb., Mem. New York Bot. Gard. 1:449. 1900. TYPE: Montana: Helena, 21 Jul 1892, *Kelsey s.n.* (Holotype: OC, not seen).—*Cirsium kelseyi* (Rydb.) Petrak, Beih. Bot. Centralbl. 35(2):548. 1917.

Carduus butleri Rydb., Bull. Torrey Bot. Club 37:542. 1910. TYPE: Montana: Big Fork, 28 Jul 1908, *B. T. Butler 674*. (Holotype: NY, not seen).—*Cirsium butleri* (Rydb.) Petrak, Beih. Bot. Centralbl. 35(2):539. 1917.

Carduus magnificus A. Nelson, Bot. Gaz. (Crawfordsville) 53:228. 1912. TYPE: Idaho: Canyon Co.: Falk's Store, 22 Jun 1910, *J. F. Macbride 271*. (Holotype: RM!; Isotypes: F, not seen, RM!).—*Cirsium magnificum* (A. Nelson) Petrak, Beih. Bot. Centralbl. 35(2):551. 1917.

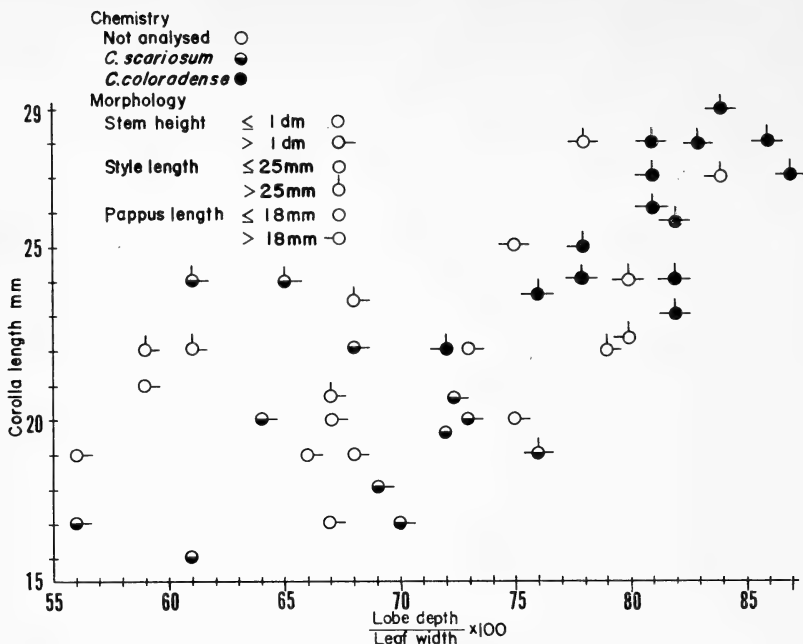


FIG. 4. Scatter diagram of morphological and chemical characteristics of *Cirsium coloradense* and *C. scariosum*.

Plants (0.5–) 4.0–6.0 (–7.0) dm tall, stems simple; heads subtended by one to several leaves [lower leaves (11–) 23–30 (–35) cm long, 2–3 cm wide, sinus depth 56–73% of leaf width, subtending leaves 11–20 cm long, 1–2 cm wide, subtire to shallowly divided], leaf bases clasping, marginal spines 4–10 mm long, generally longest on subtending leaves; heads axillary, sessile or on short peduncles (to 4 cm long), involucre 2.0–2.7 cm tall, 1.5–2.5 cm broad, about as broad as tall, with 5–8 rows of phyllaries, nonglandular; pappus 14–21 mm long; corolla white to purple, 16–24 mm long, the lobes 2–4 mm long; anthers 4–9 mm long; style 19–26 mm long, the branches 2–4 mm long; achenes 5–6 mm long, 2 mm wide, with or without a narrow yellow apical collar; flowers in early July and produces fruits by early August.

DISTRIBUTION: western one-fourth of Wyoming to Washington and Oregon and through the western half of Montana to Canada. In Wyoming (fig. 3), it is found in disturbed, moist sites, along roads and in pastures and fields; 2050–2900 m.

REPRESENTATIVE SPECIMENS: Wyoming: Fremont Co.: West side of Union Pass, 14 Aug 1894, *A. Nelson* 881; Hwy. 26–287, 4 mi E of Togwotee Pass summit, 12 Aug 1971, *Gardner* 207. Grand Teton National Park: 10 Aug 1971, *Gardner* 197A (6 dm tall), 197B (0.5 dm

tall). Johnson Co.: Headwaters of Clear Creek and Crazy Woman River, 20 Jul–15 Aug 1900, *Tweedy 3051*; Hwy. 16, 13.5 mi W of Buffalo, 15 Aug 1961, *Ownbey & Ownbey 3030*. Lincoln Co.: Moose Flats, along Gray's River, 4 Aug 1949, *C. L. Porter 5197*; Forest Route 138, 12 mi SE of jct. with Hwy. 189 (Alpine Jct.), 10 Aug 1971, *Gardner 201*. Park Co.: Clay Butte, near Beartooth Butte, 18 Aug 1951, *C. L. Porter 5924*; Hwy. 14–16–20, 7 mi E of Yellowstone National Park entrance, 10 Aug 1971, *Gardner 193*. Sublette Co.: 20 mi W of Big Piney, 11 Jul 1922, *Payson & Payson 2663*; Hwy. 189, 6.1 mi NW of Bondurant, 29 Jun 1962, *Gillett & Taylor 11612* (DAO). Teton Co.: Hoback Canyon, 11 Aug 1950, *Reed & Reed 3035*; Hwy. 26–287, 6 mi W of Togwotee Pass summit, 12 Aug 1971, *Gardner 206*. Washakie Co.: Head of Tensleep Canyon, 27 Jun 1960, *Porter & Porter 8231*; Hwy. 16, 35 mi E of Tensleep, 7 Jul 1971, *Gardner 133*. Yellowstone National Park: Snake River, 13 Aug 1899, *A. & E. Nelson 6443*; 18 mi W of east entrance, 10 Aug 1971, *Gardner 196*.

3. *CIRSIIUM DRUMMONDII* Torrey & Gray, *Flora North Amer.* 2(3):459. 1843. TYPE: Canada: "Fort Franklin on the Mackenzie River", *Richardson s.n.* (Neotype: Moore & Frankton, 1963: K, not seen). —*Cardus drummondii* (Torrey & Gray) Coville, *Contr. U. S. Natl. Herb.* 4:142. 1893.

Cirsium coccinatum Osterhout, *Torreyana* 34:45. 1934. TYPE: South Dakota: Black Hills, near Hill City, 12 Jul 1932, *G. E. Osterhout 7826*. Holotype: RM!).

Plants (1.5–) 4.0–6.0 (–7.0) dm tall, stem simple; heads seldomly subtended by one to several leaves (lower leaves 15–23 cm long, 3–4 cm wide, sinus depth variable, leaves subentire or lobed to 80% of leaf width, subtending leaves 8–13 cm long, 0.5–2.0 cm wide, generally more divided than lower leaves, rarely subentire), leaf bases clasping, marginal spine length proportional to per cent leaf division (2–4 mm long on subentire leaves, 5–10 mm long on 50–80% divided leaves), generally longest on subtending leaves; heads terminal, solitary or 2 or 3 clustered near stem apex, involucre 3.5–5.0 cm tall, 2–4 cm broad, about half as broad as tall, with 6–8 rows of phyllaries, usually glandular (this most obvious on second and third rows), glabrous or pubescent along margins; pappus 30–40 mm long; corolla purple, 39–43 mm long, the lobes 6–7 mm long; anthers 7–9 mm long; style 42–50 mm long, the branches 6–7 mm long; achenes 5 mm long and 2 mm wide with a broad (0.4–0.8 mm) apical yellow collar; flowers in late June and produces mature achenes from late July through early August.

DISTRIBUTION: Black Hills region of South Dakota and adjacent Wyoming. The species is disjunct from this area of the United States to western Canada (Moore and Frankton, 1967). The same authors state that an 1862 collection (*Hall & Harbour 343*) from northern

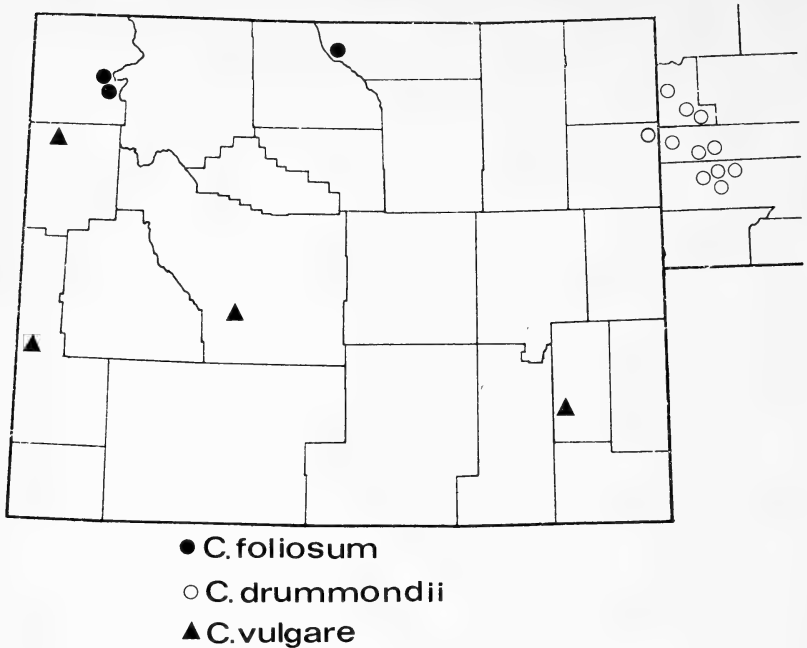


FIG. 5. Documented Wyoming distribution of *C. foliosum*, *C. drummondii* (in U. S., taxon now known only from Black Hills region), and *C. vulgare*.

Colorado is almost, if not wholly, typical of the species, and they suggest this is a relict of its range in the past. The taxon is known from two Wyoming localities (fig. 5). The locality of one collection, *A. Nelson 9442*, was visited in 1971, but the species was not found. I have not seen the other collection referred to this taxon by Moore and Frankton (1964). The locality is given as Welcome, Crook Co., Wyoming. Plants are found scattered in mesic sites, under pines and aspen; 1400–2200 m.

REPRESENTATIVE SPECIMENS: Wyoming: Weston Co.: Boyd, 19 Jul 1910, *A. Nelson 9442*.

Cirsium drummondii is distinct from all Wyoming thistles. Traditionally the species has been included in Rydberg's (1917) sect. *Foliosa*, based on the following features: heads usually in compact terminal cluster, stem simple, leaves clasping, and innermost phyllaries lacerate along the margins. The taxon does not "fit" sect. *Foliosa* due to the following characteristics: heads not noticeably exceeded by upper cauline leaves, some of the phyllaries glandular, and achenes with broad apical yellow collars; these features are characteristic of Rydberg's (1917) sect. *Undulata*. Leaf flavonoid data also suggest a similarity to the latter section (fig. 2; Tables 2 and 3). The conflicting morphological and chemical information listed above indicate the necessity for additional study to determine the closest affinities of the taxon.

4. *CIRSIUM FOLIOSUM* (Hooker) DC., Prodr. 6:654. 1838.—*Carduus foliosus* Hooker, Flora Bor. Amer. 1:303. 1833. TYPE: Canada: Alberta: "Prairies of the Rocky Mountains," *Drummond s.n.* (Holotype: K, not seen).—*Cnicus foliosus* (Hooker) A. Gray, Proc. Amer. Acad. Arts 10:40. 1874.

Plants 4–6 dm tall, stems simple; heads subtended by one to several leaves (lower leaves 15–20 cm long, 2–4 cm wide, sinus depth 60–67% of leaf width, subtending leaves 10–15 cm long, 0.5–1.0 cm wide, sinus depth 50% of leaf width), leaf bases slightly clasping, marginal spines 4–7 mm long, generally longest on subtending leaves; heads axillary on upper fourth of stem, clustered, involucre 1.9–2.5 cm tall, 1.5–2.0 cm broad, about as broad as tall, with 5–7 rows of phyllaries, nonglandular, outermost with hairs along margins; pappus 21–25 mm long, exceeding the corolla by at least 1 mm; corolla white, 19–23 mm long, the lobes 3–4 mm long; anthers 4–6 mm long; style 23–26 mm long, the branches 2–3 mm long; achenes 4 mm long, less than 2 mm wide, with a narrow yellow apical collar; flowers in late July, producing mature achenes from middle to late August.

DISTRIBUTION: northern Wyoming and adjacent Montana. Moore and Frankton (1964) indicate that it extends through western Montana, and is also known from Canada. In Wyoming (fig. 5), it is found in moist meadows and clearings; 2500–2640 m.

REPRESENTATIVE SPECIMENS: Wyoming: Sheridan Co.: Hwy. 14 alternate, 4 mi W of Burgess Jct., 9 Aug 1971, *Gardner 191*. Yellowstone National Park: Sylvan Pass, 25 Aug 1951, *Senn, Frankton & Gillett 5681* (DAO); 11 mi W of E entrance, 10 Aug 1971, *Gardner 194*.

Moore and Frankton (1967) state that *C. foliosum* is self fertile and that in the "change" from an outbreeder the corolla and anthers became smaller while the pappus retained its original length. They also suggest that *C. foliosum* arose from *C. scariosum*. The two taxa overlap considerably in corolla and anther length, however, it is the pappus length that best separates them. This suggests that rather than a reduction in the corolla and anther length of *C. foliosum* there has been an increase in the length of the pappus.

5. *CIRSIUM UNDULATUM* (Nutt.) Spreng., Syst. Veg. 3:374. 1826.—*Carduus* (§ *Cnicus*) *undulatus* Nutt., Gen. North Amer. Plants 130. 1818. TYPE: "... Lake Huron, and on the plains of the Upper Louisiana", *Nuttall s.n.* (Holotype: GH, not seen).—*Cnicus undulatus* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 10:42. 1874.

Cnicus undulatus (Nutt.) A. Gray var. *megacephalus* A. Gray, Proc. Amer. Acad. Arts 10:42. 1874. TYPE: none cited.—*Cnicus megacephalus* (A. Gray) Cockerell ex Daniels, Univ. Missouri Studies, Sci. Ser. 2(2):402. (Oct) 1911. For a more complete listing of synonymy, cf. Ownbey (1952).

Plants 4.5–8.0 dm tall, stems simple below, branching above; lower leaves 25–35 (–50) cm long, 6–10 cm wide, upper leaves 5–7 cm long, 2–4 cm wide, leaf bases clasping or decurrent (–12 mm), both leaf surfaces grayish, tomentose, more densely so below; heads terminating the branches (usually 1/branch), involucre 2.3–3.5 cm tall, 2–3 cm broad, almost as broad as tall, with 8–10 rows of phyllaries, glandular with light pubescence along margins; pappus 25–30 mm long; corolla pink to purple, 34–40 mm long, the lobes 9–10 mm long; anthers 12–14 mm long; style 36–42 mm long, the branches 5–6 mm long; achenes 6 mm long, 2–3 mm wide, with or without a narrow yellow apical collar; flowers in early July, producing fruits from late July throughout August.

DISTRIBUTION: Michigan to Texas and Arizona to British Columbia. In Wyoming (fig. 6), the taxon is a roadside weed and occasionally is found in fields and pastures; 1130–2720 m.

REPRESENTATIVE SPECIMENS: Wyoming: Albany Co.: Laramie, City Park, 2 Oct 1894, *A. Nelson 1156*; Hwy. 34, 6 mi E of Morton's Pass, 2 Jul 1971, *Gardner 118*. Campbell Co.: near Spotted Horse, 24 Jul 1958, *Porter & Porter 7580*. Crook Co.: 17 mi S of Sundance, Inyankara

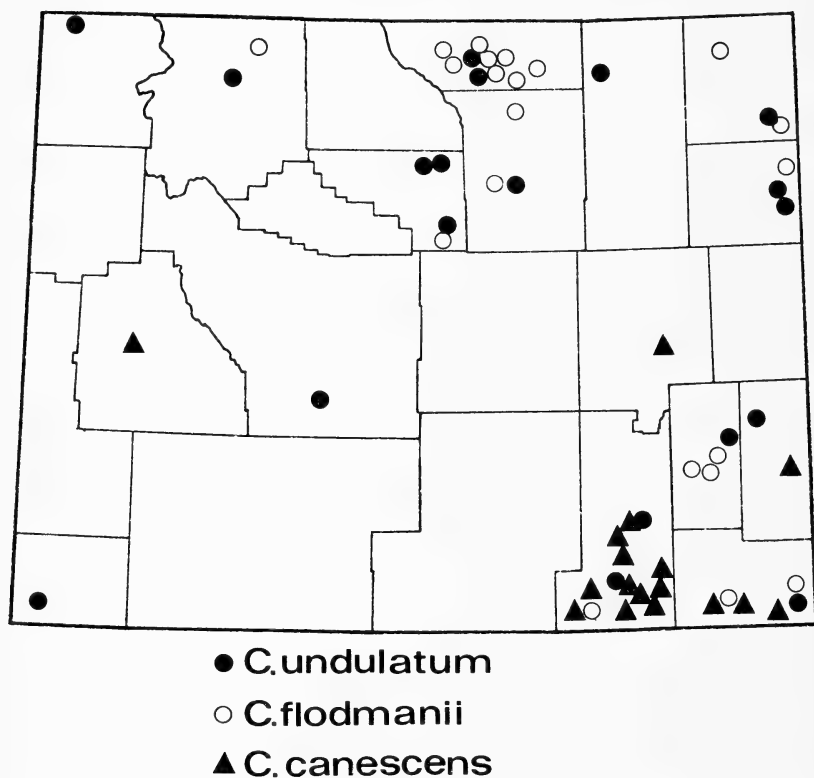


FIG. 6. Documented Wyoming distribution of *C. undulatum*, *C. flodmanii*, and *C. canescens*.

Creek, 14 Jul 1927, *Hayward* 2138. Fremont Co.: Hwy. 287-789, 5 mi E of jct. with Hwy. 28, 17 Aug 1971, *Gardner* 213. Goshen Co.: Haystack Range, 8 Jul 1955, *C. L. Porter* 6746. Johnson Co.: Hwy. 87, 14 mi S of Buffalo, 9 Aug 1971, *Gardner* 187. Laramie Co.: Pine Bluffs, 5 Jul 1897, *A. Nelson* 3506. Park Co.: Sunlight Valley, Crandall Creek road, 23 Aug 1924, *Pearson & Pearson* 196. Platte Co.: Hwy. 317, Lake Guernsey State Park, 2 Jul 1971, *Gardner* 120. Sheridan Co.: between Sheridan & Buffalo, 15 Jun-15 Jul 1900, *Tweedy* 3049; Hanna Creek, 28 Jun 1909, *Vie Willits* 195. Unita Co.: Evanston, Jul-Aug 1938, *Myroie* 3. Washakie Co.: Hwy. 16, 13 mi NE of Tensleep, 16 Aug 1961, *Ownbey & Ownbey* 3036; Hwy 16, 25 mi E of Tensleep, 7 Jul 1971, *Gardner* 130. Weston Co.: Newcastle, 9 Jul 1927, *Hayward* 2010; Hwy. 16, 1 mi NW of Wyoming-South Dakota border, 5 Aug 1971, *Gardner* 175. Yellowstone National Park: Mammoth Hot Springs, 20 Jul 1899, *A. & E. Nelson* 6027, 6028.

The most useful character in separating *C. undulatum* and the somewhat similar *C. flodmanii* is the presence of a wide apical collar on the achenes of *C. flodmanii*. This collar is very narrow or lacking in *C. undulatum*. Other characters include rosette leaves entire, upper leaf surface greenish, for *C. flodmanii*, and rosette leaves divided, upper leaf surface grayish, for *C. undulatum*. Frankton and Moore (1961) state that the hairs on the filaments of *C. flodmanii* are longer and denser than those of *C. undulatum*.

6. *CIRSIUM FLODMANII* (Rydb.) Arthur, *Torrey* 12:34. 1912.—*Carduus flodmanii* Rydb., *Mem. New York Bot. Gard.* 1:451. 1900. TYPE: Montana: East Gallatin Swamps, 1896, *Flodman* 879. (Holotype: NY, not seen).

Carduus oblancoelatus Rydb., *Bull. Torrey Bot. Club* 28:510-511. 1901. TYPE: Colorado: Twin Lakes, 1896, *F. Clements* 385. (Holotype: NY?, not seen). *Cirsium oblancoelatum* (Rydb.) K. Schum., *Bot. Jahresber. (Just)* 29(1):566. 1903.—*Cirsium flodmanii* (Rydb.) Arthur f. *oblancoelatum* (Rydb.) D. Löve & Bernard, *Svensk Bot. Tidskr.* 53(4):450-451. 1959.

Plants 3.5-7.0 dm tall, stems simple below (rarely two or three from the same rootstock), branching above; lower leaves 28-33 cm long, 3-8 cm wide, usually at least one rosette leaf is entire, leaf bases clasping, lower leaf surfaces grayish, upper surfaces green, glabrous or with thin tomentum; heads terminating the branches (usually 1/branch) involucre 2.1-3.5 cm tall, 1-2 cm broad, about half as broad as tall, with 8 rows of phyllaries, glandular, outermost arachnoid pubescent, inner ones hairy along margins; pappus 25 mm long; corolla purple, 28-31 mm long, the lobes 6-7 mm long; anthers 9-11 mm long; style 31-32 mm long, the branches 5-6 mm long; achenes 4-5 mm long, 2 mm wide, with a broad (0.4-0.7 mm) yellow apical collar; flowers from June to August and producing mature achenes throughout August.

DISTRIBUTION: Colorado to northeastern Iowa and from Colorado and Iowa into Canada. In Wyoming (fig. 6), the species occurs mainly in moist areas, where land is irrigated and/or cultivated; 1100–2100 m.

REPRESENTATIVE SPECIMENS: Wyoming: Albany Co.: Cummins, 30 Jul 1895, *A. Nelson* 1563. Big Horn Co.: Red Banks, 22 Jul 1901, *Goodding* 335. Crook Co.: Inyankara Mt., 21 Aug 1897, *Griffiths* s.n. (RM-70552); New Haven, 2 Aug 1924, *Kendall* 10776. Johnson Co.: Hwy. 16, 3 mi NE of Buffalo, 7 Jul 1971, *Gardner* 136A (flower), 136B (bud); Hwy. 87, 23 mi S of Buffalo, 9 Aug 1971, *Gardner* 186. Laramie Co.: Cheyenne, 11 Aug 1891, *Buffum* s.n. (RM-1838); near Pine Bluffs, on Spring Creek, 14 Aug 1959, *Porter & Porter* 8028. Park Co.: Clark's Fork Valley, Little Rocky Crossing, 24 Aug 1924, *Pearson & Pearson* 202, 203. Platte Co.: Wheatland, 2 Sep 1903, *A. Nelson* 8981; Hwy. 87, 1.8 mi N of Wheatland, 13 Sep 1959, *Ownbey & Ownbey* 1304. Sheridan Co.: Sheridan, 10 Jul 1896, *A. Nelson* 2272; between Sheridan and Buffalo, 15 Jun–15 Jul 1900, *Tweedy* 3050; 5 mi NW of Big Horn, road between Big Horn and Becton, 9 Aug 1971, *Gardner* 188. Weston Co.: Near old Boyd Townsite, E of Four Corners Store, 9 Aug 1971, *Gardner* 176.

Carduus oblanceolatus Rydb. was described as being closest to *C. flodmanii*, differing in the narrower phyllaries, and all leaves being entire. D. Löve and Bernard (1959) considered it to be only a form of *C. flodmanii* and made the transfer as forma *oblanceolatum* (Rydb.) D. Löve & Bernard. The plants that "fit" forma *oblanceolatum* have the same geographical distribution as *C. flodmanii*. In Wyoming specimens, a continuous variation is seen, and I feel there is no taxonomic value in recognizing f. *oblanceolatum*.

7. *CIRSIIUM OCHROCENTRUM* A. Gray, Mem. Amer. Acad. Arts (n.s.) 4:110. 1849. TYPE: New Mexico: Mountain-sides, around Santa Fe, Jul?, *Fendler* 486. (Holotype: GH, not seen).—*Cnicus ochrocentrus* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 19:57. 1883.—*Carduus ochrocentrus* (A. Gray) Greene, Proc. Acad. Nat. Sci. Philadelphia 1892:363. 1893.—*Cnicus undulatus* Nutt. var. *ochrocentrus* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 10:42–43. 1874.—*Carduus undulatus* Nutt. var. *ochrocentrus* (A. Gray) Rydb., Contr. U. S. Natl. Herb. 3:510. 1896.

Plants 4.0–7.6 dm tall, stems simple below (rarely two from a single root), branching above; lower leaves 12–22 cm long, 2.5–3.5 cm wide, upper leaves 5–6 cm long, 1–2 cm wide, leaf bases decurrent, usually greatest on upper leaves, the wings 20–25 mm long near stem apex, 8–17 mm long near ground level; heads terminating the branches (usually 1/branch), involucre 3.0–3.5 (–4.2) cm tall, 1.5–2.5 cm broad, 1/2 to 2/3 as broad as tall, with 7 or 8 rows of phyllaries, obscurely glandular, with light pubescence along margins; pappus 27–30 mm long; corolla

white to pink, 34–38 mm long, the lobes 8–9 mm long; anthers 11–13 mm long; style 35–45 mm long, the branches 5–7 mm long; achenes 6–7 mm long and 2.5–3.0 mm wide, with or without a narrow yellow apical collar; flowers in mid-August, and produces mature achenes by the end of the month.

DISTRIBUTION: Nebraska to Texas and Arizona. In Wyoming (fig. 7), the species is often seen as a roadside weed, and in fields in relatively dry sites; 1320–2100 m.

REPRESENTATIVE SPECIMENS: Wyoming: Albany Co.: Hwy. 30, 8 mi NW of Rock River, 9 Aug 1971, *Gardner 182*. Carbon Co.: Hwy. 30, 2 mi SE of Medicine Bow, 9 Aug 1971, *Gardner 183*. Fremont Co.: Hwy. 287–26, 7.9 mi SE of Crowheart, 16 Aug 1961, *Ownbey & Ownbey 3037*; Hwy. 26–287, 17 mi NW of Lander, 12 Aug 1971, *Gardner 209*. Goshen Co.: Fort Laramie, 26 Jul 1908, *A. Nelson 9196*; Hwy. 85, 15 mi N of Lingle, 5 Aug 1971, *Gardner 177*. Laramie Co.: 7 mi W of Cheyenne and 1 mi N of Hwy. US 30, 11 Aug 1958, *Jean Finzel 109*; Hwy. I-25, 15 mi S of Chugwater, 30 Jul 1971, *Gardner 155*. Niobrara Co.: Manville, 31 Aug 1944, *Pfadt s.n. (RM-197375)*. Platte Co.: Hwy. 34, 3 mi

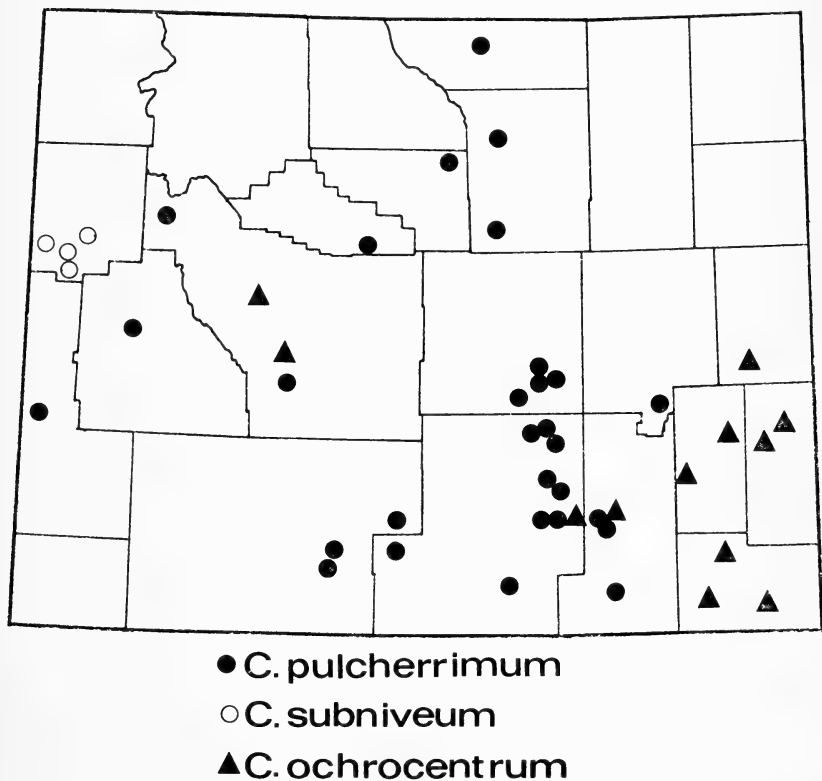


FIG. 7. Documented Wyoming distribution of *C. pulcherrimum*, *C. subniveum*, and *C. ochrocentrum*.

E of Sybille Creek, 2 Jul 1971, *Gardner 119*; Hwy. 26, 12 mi E of jct. with Hwy. I-25, 2 Jul 1971, *Gardner 121* (3.5 dm tall), 122 (7 dm tall).

With decurrent leaves, involucre 3 cm or more tall, and broad triangular phyllaries tipped by stout spines, this taxon is almost impossible to confuse with any other Wyoming thistle. The cauline leaves appear slightly wilted and seem to droop. This feature is particularly useful in the field, but is often obscured on mounted specimens.

8. *CIRSIUM CANESCENS* Nutt., Trans. Amer. Philos. Soc. 7:420. 1841. TYPE: "Arid plains of upper Platte", *Nuttall s.n.* (Holotype: BM, not seen).

Cnicus nelsoni Pammel, Proc. Iowa Acad. Sci. 8:235. 1901. TYPE: Wyoming: Albany Co.: Laramie, Aug 1900, *A. Nelson 8093*. (Holotype: ISC, not seen; Isotype: RM!).—*Carduus nelsonii* (Pammel) A. Nelson in Coulter and Nelson, Manual Bot. Rocky Mts. 586. 1909.—*Cirsium nelsoni* (Pammel) Petrak, Beih. Bot. Centralbl. 35(2):552. 1917.—*Cirsium nelsonii* (Pammel) Rydb., Flora Rocky Mts. and Adjacent Plains 1012, 1069. 1917. For a more complete listing of synonymy, cf. Ownbey (1952).

Plants 4.0–6.5 (–9) dm tall, stems simple below, branching above; lower leaves 18–32 cm long, 5–8 cm wide, upper leaves 3–7 cm long, 0.3–2.0 cm wide, leaf bases decurrent, usually greatest on upper leaves, the wings 17–25 mm long near stem apex, 5–22 mm long near ground level; heads terminating the branches (usually 1/branch), involucre 1.8–2.6 cm tall, and 1.8–2.6 cm broad, about as broad as tall, with 6–8 rows of phyllaries, glandular, with light pubescence along margins; pappus 19–21 mm long; corolla white (rarely pink to purple), 24–28 mm long, the lobes 6 mm long; anthers 9.5–10.0 mm long; style 26–33 mm long, the branches 5–6 mm long; achenes 5–7 mm long, 2.5 mm wide, with or without a narrow yellow apical collar; flowers in late June to late July and produces mature achenes from late July to late August.

DISTRIBUTION: Saskatchewan to Iowa, west to Wyoming, Utah and New Mexico. In the state (fig. 6), it is found as a roadside weed in dry habitats; 1560–2560 m.

REPRESENTATIVE SPECIMENS: Wyoming: Albany Co.: Laramie Hills, 7 Jul 1894, *A. Nelson 414*; Jelm, "Plains and Foothills", *A. Nelson 8071* (Paratype of *Cnicus nelsoni* Pammel, RM!). Converse Co.: 0.7 mi N of Douglas, 21 Jul 1951, *Ownbey & Ownbey 1572*. Fremont Co.: Porcupine, Wind River, *T. A. Williams s.n. (RM-68200)*. Goshen Co.: Hwy. 26, 4.9 mi NW of Lingle, 20 Jul 1951, *Ownbey & Ownbey 1567*. Laramie Co.: Hwy. I-80, 7 mi W of Cheyenne, 20 Jul 1971, *Gardner 156A*; Hwy. 214, 1 mi S of Hwy. I-80 Burns-Carpenter exit, 3 Aug 1971, *Gardner 168*. Sublette Co.: Hwy 189, 10 mi N of Big Piney, 10 Aug 1971, *Gardner 204A*.

Cirsium canescens is characterized by decurrent leaves, involucre

about as broad as tall, lobes of lower leaves 3.5–5.0 times longer than broad, and short (usually less than 4 cm long) spines on the phyllary tips. It is most commonly confused with *C. pulcherrimum*. The latter taxon is differentiated by involucre about half as broad as tall, lobes of lower leaves 3.0 or less times longer than broad, and phyllary spines 5 mm or more long.

9. *CIRSIUM PULCHERRIMUM* (Rydb.) K. Schum., Bot. Jahresber. (Just) 29(1):566. 1903.—*Carduus pulcherrimus* Rydb., Bull. Torrey Bot. Club 28:510. 1901. TYPE: Wyoming: Headwaters of Clear Creek and Crazy Woman River, 1900, *Tweedy 3048*. (Holotype: NY, not seen; Isotype: RM!).

Plants 4.5–6.0 (–8.0) dm tall, stems simple below, branching above, frequently several stems from one rootstock; lower leaves 12–22 cm long, 1.5–6.0 cm wide, upper leaves 4–7 cm long, 0.5–2.5 cm wide, leaf bases decurrent, usually greatest on upper leaves, the wings 15–35 mm long near stem apex, 4–17 mm near ground level, lower leaf surfaces grayish, upper surfaces green or with scattered tufts of hair; heads terminating the branches, but occasionally sessile in axils of middle cauline leaves, involucre 1.8–2.7 cm tall, 1.0–1.5 (–2.0) cm broad, 1/2 to 2/3 as broad as tall, with 6 or 7 rows of phyllaries, glandular, glabrous to pubescent along margin; pappus 15–18 mm long; corolla pink to purple, 18–25 mm long, the lobes 4–6 mm long; anthers 7–9 mm long; style 21–24 (–26) mm long, the branches 3–5 mm long; achenes 5–6 mm long, 2–3 mm wide, with a narrow yellow apical collar; flowers in late June to late July, producing fruits from early July to early August.

DISTRIBUTION: Frequent in Wyoming (fig. 7), as a roadside weed and less commonly in pastures and fields; 1440–2800 m. The distribution outside Wyoming is poorly known, since the taxon has generally been included in *C. subniveum* (see discussion below).

REPRESENTATIVE SPECIMENS: Wyoming: Albany Co.: Medicine Bow, 1898, *E. Nelson 4396*, (Paratype: RM!); Hwy. 30, 8 mi NW of Rock River, 9 Aug 1971, *Gardner 181*. Carbon Co.: 7 mi N of Medicine Bow, 9 Aug 1971, *Gardner 185*; 5 mi NW of Shirley Basin townsite, 6 Jul 1971, *Gardner 126A-D* (leaf pubescence variable). Converse Co.: 8 mi SW of Esterbrook, road to Fort Fetterman Road, 2 Jul 1971, *Gardner 123*. Fremont Co.: 10 mi S of Lander, Brown Canyon, 24 Jul 1961, *Fisser 636*; Hwy. 26–287, 10 mi W of Dubois, 12 Aug 1971, *Gardner 208*. Hot Springs Co.: 30 mi SE of Thermopolis, 8 Jul 1958, *Allen s.n.* (RM-28800-s). Johnson Co.: Hwy. 16, 10 mi W of Buffalo, 15 Aug 1961, *Owney & Owney 3029A*; 12 mi S of Hwy. I-25, on TTT Ranch Road, 7 Jul 1971, *Gardner 140*. Lincoln Co.: E of Smoot, near Cottonwood Lake, 28 Jul 1923, *Payson & Armstrong 3614*. Natrona Co.: Casper Mtn., Circle Drive, 9 Aug 1957, *C. L. Porter 7417*; Hwy. 487, 10 mi S of jct. with Hwy. 220, 6 Jul 1971, *Gardner 127*. Sheridan Co.: Upper Grade, 9 Jul 1909, *Vie Willits 276*; Bondi Camp, W of Sheridan, 7 Aug

1938, *Hapeman s.n.* (RM-223374). Sublette Co.: Hwy. 189, 10 mi N of Big Piney, 10 Aug 1971, *Gardner 204B*. Sweetwater Co.: Bitter Creek, 12 Jul 1897, *A. Nelson 3529*; Hwy. 789, 5 mi S of Creston Jct., 22 Jul 1971, *Gardner 153*. Washakie Co.: Hwy. 16, 30 mi E of Tensleep in Tensleep Canyon, 7 Jul 1971, *Gardner 131 & 132*; Hwy. 16, 15 mi W of Buffalo, 7 Jul 1971, *Gardner 134 & 135*.

Rydberg (1917) recognized *C. pulcherrimum* and *C. subniveum* as distinct species. Since then, the binomial *Cirsium pulcherrimum* seldom appears either in the literature or on herbarium labels, the plants mostly being referred to *C. subniveum*. Cronquist (1955) includes *C. subniveum* in his treatment, but concludes the specimens he has seen differ from the type of *C. subniveum* in being less densely hairy, and that possibly his plants need another name. After studying the type material of both taxa, Moore and Frankton (1963) suggested that there is some justification for relegating *C. subniveum* to synonymy under *C. pulcherrimum*. However, they point out that the type of the former taxon has been damaged by insects and that corolla and pappus characters are obscure, while achenes, anthers, and styles are not available. Isotypes of both taxa are deposited at RM, and have not been damaged by insects, thus structures that are obscure or lacking on the holotypes are in excellent condition on these isotypes. Although the two taxa are not distinct in every character, it is possible to distinguish them by considering a combination of features. *Cirsium pulcherrimum* is characterized by having the decurrence of the upper leaves greater than, or equal to, that of the lower leaves, while the reverse is true in *C. subniveum*, i.e., the lower leaves are always more decurrent than the upper ones. In addition to the floral characteristics used to separate the two taxa (fig. 8), *C. pulcherrimum* has generally longer phyllaries and spines, while *C. subniveum* is more densely hairy on the leaf surfaces and on the phyllaries. In Figure 8 the specimen represented near coordinates 10×25 falls within the range of *C. subniveum*. Characteristics not plotted that indicate that this gathering is *C. pulcherrimum* include glabrous upper leaf surface and phyllaries, and decurrence of upper leaves greater than that of the lower ones. By combining these morphological data with the chemical data, this collection is unquestionably *C. pulcherrimum*.

Both taxa have $2n = 34$ (Moore and Frankton, 1963; Ownbey and Hsi, 1969; Table 1). Ownbey and Hsi (1963) give $2n = 32$ for *C. subniveum*, but question the proper identification of the specimen from which the count was obtained. *Cirsium subniveum* (fig. 1) has six satellite chromosomes, while *C. pulcherrimum* (fig. 1) apparently has none. The species are also distinct chemically (fig. 2).

10. *CIRSIIUM SUBNIVEUM* Rydb., Flora Rocky Mts. and Adjacent Plains 1006, 1068. 1917. TYPE: Wyoming: Teton Co.: Jackson's Hole, 21 Aug 1894, *A. Nelson 1070*. (Holotype: US, not seen; Isotype: RM!)

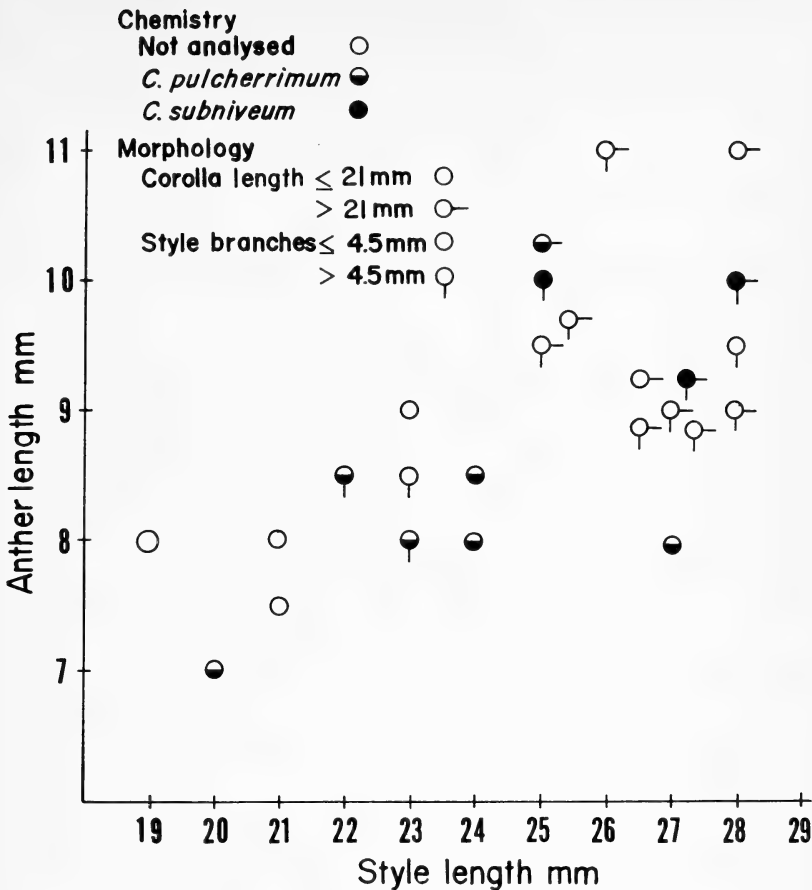


FIG. 8. Scatter diagram of morphological and chemical characteristics of *Cirsium pulcherrimum* and *C. subniveum*.

Plants 3.5–8.0 dm tall, stems simple below, branching above; lower leaves 20–25 cm long, 3–5 cm wide, all leaves more or less decurrent, this most pronounced on the lower ones, the wings 5–10 mm long near stem apex, 25–40 mm long near ground level, both leaf surfaces tomentose, the tomentum becoming somewhat looser on upper surfaces; heads terminating the branches, but occasionally sessile in axils of cauline leaves, involucre 1.8–2.4 cm tall, and 1.0–1.6 cm broad, about half as broad as tall with 5–7 rows of phyllaries, glandular or not, arachnoid pubescent; pappus 15–20 mm long; corolla white to purple, 20–26 mm long, the lobes 3–4 mm long; anthers 9–11 mm long; style 26–33 mm long, the branches 4–6 mm long; achenes 5.5–6.5 mm long, 2.0–2.5 mm wide, with a narrow yellow apical collar; flowers in late July through early August, producing fruits from mid-August onward.

DISTRIBUTION: Oregon, Nevada, and central Idaho to northwestern

Wyoming. In Wyoming (fig. 7), the habitat of the species is variable, as it was collected under *Populus* and *Salix* in one area and as a roadside weed in another; 1880–2100 m.

REPRESENTATIVE SPECIMENS: Wyoming: Grand Teton National Park: Gros Ventre Campground, 10 Aug 1971, *Gardner 199*. Sublette Co.: 20 mi W of Big Piney, 11 Jul 1922, *Payson & Payson 2656*. Teton Co.: 3 mi NE of Jackson, 17 Aug 1961, *Ownbey & Ownbey 3040*; jct. Hwys. 26–89 & 187–189, Hoback Jct., 10 Aug 1971, *Gardner 200*.

11. *CIRSIIUM TWEEDYI* (Rydb.) Petrak, Beih. Bot. Centralbl. 35(2):560. 1917.—*Carduus tweedyi* Rydb., Mem. New York Bot. Gard. 1:499. 1900. TYPE: Montana: Park Co.: 1887, *Tweedy 350*. (Holotype: NY, not seen).

Cirsium hookerianus (Nutt.) Heller var. *eriocephalus* A. Nelson in Coulter and Nelson, Manual Bot. Rocky Mts. 585. 1909. *pro parte*. *Carduus polyphyllus* Rydb., Bull. Torrey Bot. Club 37:542. 1910. TYPE: Montana: Mountains near Indian Creek, 21 Jul 1896, *Rydberg & Bessey 5216*. (Holotype: NY, not seen).—*Cirsium polyphyllum* (Rydb.) Petrak, Beih. Bot. Centralbl. 35(2):556. 1917.

Plants (1.5–) 2.0–4.5 (–6.0) dm tall, stems simple; lower leaves 19–23 cm long, 2–4 cm wide, subtending leaves 4–11 cm long, 0.5–1.0 (–1.3) cm wide, leaf bases decurrent, wings to 30 mm long; heads clustered near stem apex, rarely axillary on upper half of plant, involucre 1.5–3.0 cm tall, and 1.0–1.5 cm broad, 1/2 to 2/3 as broad as tall, with 5–7 rows of phyllaries, nonglandular (one specimen seen with a few glandular phyllaries), the outermost rows arachnoid pubescent (this occasionally true of all phyllaries) or rarely glabrous; pappus 10–18 mm long; corolla white to pink, 16–25 mm long, the lobes 5–7 mm long; anthers 8–9 mm long; style 21–29 mm long, the branches 4.5–5.0 mm long; achenes 6 mm long, 2 mm wide, with or without a narrow yellow apical collar; flowers in early August and produces mature achenes from late August through early September.

DISTRIBUTION: northern Colorado through Wyoming to north central Montana and west to adjacent Idaho. In Wyoming (fig. 9), the species is found on disturbed, usually gravelly soils; 2130–3450 m.

REPRESENTATIVE SPECIMENS: Wyoming: Big Horn Co.: Medicine Wheel, 1 Aug 1931, *Solheim 463*; Hwy. alternate 14, 35 mi E of Lovell, road to Medicine Wheel, 9 Aug 1971, *Gardner 192*. Fremont Co.: Two Ocean Mt., 10,000 ft, 9 Sep 1948, *Reed & Reed 2568*; Gannett Peak area, W of Dinwoody Creek, 12,000 ft, 6 Aug 1963, *Jozwik 474*. Grand Teton National Park: W of Jenny Lake, Mt. Woodring, 9 Aug 1963, *Merkle 63–72*. Park Co.: Hwy. 312, 17.6 mi SW of Montana-Wyoming state line, 2 Sep 1961, *Ownbey & Ownbey 3073*. Sheridan Co.: Little Goose Creek Hills, 16 Jul 1896, *A. Nelson 2339*; Hwy. 14, 8 mi E of Burgess Jct., 9 Aug 1971, *Gardner 190*. Sublette Co.: Green River Lakes,

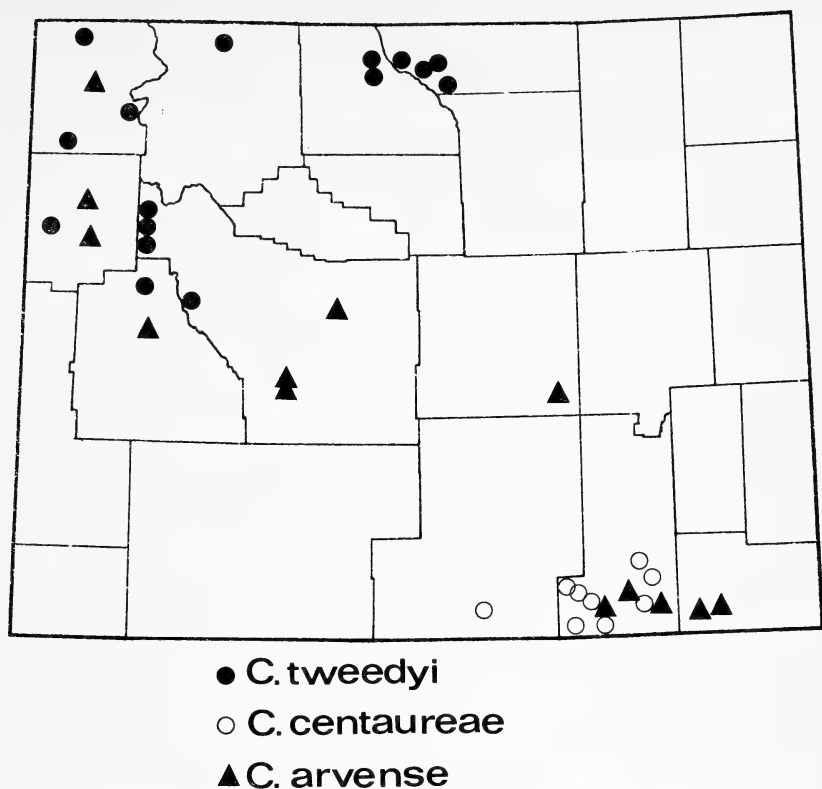


FIG. 9. Documented Wyoming distribution of *C. tweedyi*, *C. centaureae*, and *C. arvense*.

White Rock Mt., 8 Aug 1925, *Payson & Payson* 4610. Yellowstone National Park: Snake River, 12 Aug 1899, *A. & E. Nelson* 6419; 5.5 mi W of east entrance, E side of Sylvan Pass, near summit, 10 Aug 1971, *Gardner* 195.

Cirsium tweedyi is apparently the only species of Rydberg's (1917) sect. *Eriocephala* in Wyoming. Moore and Frankton (1965) suggest that *C. scopulorum* (Greene) Cockerell may reach the south central portion of the state, but attempts to find it west of Encampment in the Sierra Madre Range were unsuccessful. A third species, *C. polyphyllum*, has been reported from northwestern Wyoming. This species is reported from the same habitats and general distribution as *C. tweedyi* and morphologically the two intergrade considerably. Moore and Frankton (1965) place these species in synonymy, a conclusion with which I agree.

12. *CIRSIIUM CENTAUREAE* (Rydb.) K. Schum., Bot. Jahresber. (Just) 29(1):566. 1903.—*Carduus centaureae* Rydb., Bull. Torrey Bot.

Club 28:507. 1901. TYPE: Colorado: Larimer Co.: [as Laramie Co.] 1895, *J. H. Cowen s.n.* (Holotype: NY, not seen).—*Cirsium centaureae* (Rydb.) Cockerell ex Daniels, Univ. Missouri Studies, Sci. Ser. 2(2):402. (Oct.) 1911. (Note: combination already made by K. Schum., 1903.)

Cnicus carlinoides Schrank var. *americanus* A. Gray, Proc. Amer. Acad. Arts 10:48. 1874. TYPE: Colorado Territory: Rocky Mts., *Hall & Harbour* 342. (Holotype: GH?, not seen).—*Cnicus americanus* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 19:56. 1884.—*Carduus americanus* (A. Gray) Greene, Proc. Acad. Nat. Sci. Philadelphia 1892:363. 1893.—*Cirsium americanum* (A. Gray) Daniels, Univ. Missouri Studies, Sci. Ser. 2(2):401. (Oct.) 1911. non K. Schum., 1903.

Plants (3.0–) 6.0–8.5 dm tall, stems simple or several from the base, branching above; lower leaves 19–27 cm long, 4–9 cm wide, upper leaves 5–6 cm long, 1 cm wide, leaf bases decurrent, usually greatest on upper leaves, wings 25–35 mm long near stem apex, 10–17 mm long near ground level; heads terminating the branches (usually 1/branch), involucre 1.9–2.7 cm tall, 0.8–1.3 cm broad, about half as broad as tall, with 5–7 rows of phyllaries, margins membranous and lacerate, non-glandular; pappus 10–18 mm long; corolla white to pink, 16–23 mm long, the lobes 4–5 mm long; anthers 8–10 mm long; style 10–18 mm long, the branches 4–5 mm long; achenes 5.5–8.0 mm long, 2.0–2.5 mm wide, with or without a narrow yellow apical collar; flowers in late July, producing mature achenes throughout August.

DISTRIBUTION: California, Oregon, and Washington, and also from Utah, Colorado, and Wyoming. In Wyoming (fig. 9), the taxon is found in moist sites, under deciduous trees and rarely as a roadside weed; 2320–3130 m.

REPRESENTATIVE SPECIMENS: Wyoming: Albany Co.: Cummins, 29 Jul 1895, *A. Nelson 1512*; County road 17, 5 mi SE of quarry, 19 Jul 1971, *Gardner 143*. Carbon Co.: Bridger Peak, 24 Aug 1903, *Goodding 2009*.

Cirsium centaureae is easily recognized by its broadly dilated, lacerate phyllaries, freely branched stem, and leaf bases that are strongly decurrent, with laterally expanded wings.

13. *CIRSIIUM VULGARE* (Savi) Airy-Shaw, Fedde Rep. Sp. Nov. 43:303. 1938.—*Carduus vulgaris* Savi, Flora Pisana 2:241. 1798. (Pisa, Italy) (Holotype: none cited). For a more complete listing of synonymy cf. Cronquist (1955).

Plants 6–15 dm tall, stems simple below, branching above; lower leaves 15–20 cm long, 3–5 cm wide, upper leaves 3–7 cm long, 2 cm wide, leaf bases decurrent, wings 20–35 mm long, about the same throughout plant, upper leaf surfaces green, with appressed 0.5–1.0 mm long spines

on surface; heads in clusters at ends of branches or solitary, to 5 cm tall, involucre 3.0–3.5 cm tall, 1.8–2.3 cm broad, about $2/3$ as broad as tall, with 9–12 rows of phyllaries, all reflexed near middle, nonglandular, with light arachnoid pubescence; pappus 25–28 mm long; corolla purple, 27–33 mm long, the lobes 5–6 mm long, anthers 7–8 mm long; style 29–35 mm long, the branches 4–5 mm long, achenes 4 mm long, 1.5 mm wide, with or without a narrow yellow apical collar; flowers in late July, and produces fruits throughout August.

DISTRIBUTION: a European introduction, occurring over most of the United States. In Wyoming (fig. 5), the species is found as a roadside weed, in dry sites; 1440–2130 m.

REPRESENTATIVE SPECIMENS: Wyoming: Fremont Co.: N of Lander, 17 Sep 1941, *A. & R. Nelson 4982*. Grand Teton National Park: 6 mi N of Coulter Bay, 16 Aug 1961, *Porter & Porter 8836*. Lincoln Co.: 15 mi S of Afton, 25 Aug 1945, *C. L. Porter 3820*. Platte Co.: W of Wheatland, Palmer Canyon road, 6 Aug 1959, *Porter & Porter 8002*.

Cirsium vulgare is easily recognized because it is the only species in Wyoming with spines on upper leaf surfaces. The reflexed aspect of the phyllaries is also unique for Wyoming species of the genus.

14. *CIRSIUM ARVENSE* (L.) Scop., *Flora Carn.* (ed. 2) 2:126. 1772.—*Serratula arvenis* L., *Sp. Pl.* 820, 1753. TYPE: "*Habitat in Europae cultis agris*". For a more complete listing of synonymy, cf. Hegi, *Illus. Flora von Mittel-Europa*, 903. 1928.

Plants 2.5–5.5 dm tall, stems simple below, usually freely branching above; lower leaves 8–10 cm long, 2–5 cm wide, uppermost leaves greatly reduced, 1.5–2.0 cm long, 0.5–1.0 cm wide, leaf bases decurrent on lower $2/3$ of plant (wings 10–20 mm long), upper leaves clasping; heads in loose clusters, corymbiform, involucre (0.9–) 1.2–1.7 (–2.0) cm tall, and 0.6–1.0 cm broad, about $1/2$ as broad as tall, with 5 or 6 rows of phyllaries, glandular, with light pubescence along margins; pappus 12–23 mm long; corolla pink to purple (rarely white), 14–18 mm long, the lobes 4–5 mm long; if pappus is longer than corolla, the anthers are 1–2 mm long, if pappus is shorter than the corolla, the anthers are 4–5 mm long (apparently dioecious); style 16–19 mm long, the branches 1–2 mm long; achenes 2–4 mm long, 1.0–1.5 mm wide, with a narrow yellow apical collar; flowers from late July to early September, producing fruits from early August onward.

DISTRIBUTION: an introduction from Europe, the species is widespread in the United States. In Wyoming (fig. 9), it occurs in a wide range of habitats, but is usually seen as a roadside weed in dry sites; 1160–2560 m.

REPRESENTATIVE SPECIMENS: Wyoming: Albany Co.: 5 mi W of Laramie, 16 Aug 1947, *C. L. Porter 4394*; County road 37, 3 mi S of jct. with Hwy. 230, 6 Aug 1971, *Gardner 179*. Fremont Co.: near Lander,

20 Aug 1934, *Rollins* 765; Popo-Agie River, S of Lander city limits, 2 Aug 1965, *Scott* 593. Grand Teton National Park: 5 mi E of Hwy. 26-89, road to Kelly, 10 Aug 1971, *Gardner* 198. Laramie Co.: Cheyenne, 1901, *A. Nelson s.n. (RM-37173)*; 7 mi W of Cheyenne, 1 mi N of Hwy. US 30, 19 Aug 1959, *Jean Finzel* 395. Natrona Co.: Casper Mt., Gothmore Loop, 17 Aug 1962, *Jozwik* 312. Sheridan Co.: Sheridan Expt. Farm, Sep 1895, *Lewis* 20; Sheridan, 4 Aug 1926, *A. Nelson* 10745. Sublette Co.: 3 mi SW of Pinedale, 13 Jul 1966, *Watson* 66-17. Teton Co.: Jackson Hole Wildlife Park, 19 Aug 1947, *Reed & Reed* 1653. Yellowstone National Park: Central Plateau, 29 Aug 1967, *Taylor* 67-141.

Morphologically the species is quite distinct, producing capitula in a corymbiform capitulescence. The heads are very small, and the flowers of some apparently are functionally pistillate and have greatly reduced anthers. Others appear to have functional anthers, but I have never found mature achenes in these and question whether they have functional pistils. Usually an individual plant produces only one head type.

ACKNOWLEDGMENTS

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EVIDENCE FOR THE HYBRID ORIGIN OF *CERCIDIUM SONORAE* (LEGUMINOSAE: CAESALPINIOIDEAE) OF NORTHWESTERN MEXICO

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Cercidium sonorae Rose & Johnston, one of the five members of the genus occurring in the Sonoran Desert, is found only within the distributional overlap of *C. microphyllum* (Torr.) Rose & Johnston and *C. praecox* (Ruiz & Pavón) Harms (fig. 1). Trees of *C. sonorae* are less abundant than those of either *C. microphyllum* or *C. praecox*; when they do occur, however, one or the other, or both, of the other two taxa have been noted to be somewhere in the vicinity. This distributional pattern and the morphological intermediacy of *C. sonorae* between *C. microphyllum* and *C. praecox* led to the hypothesis of its hybrid origin. *Cercidium molle* Johnston, known only from the type collection (Johnston 3877, Agua Verde Bay, Baja California, México) is considered to fall within the variational range of *C. sonorae* (Carter, 1974).

Cercidium microphyllum is a tree up to 8 m tall, with ascending branches that lend it a broomlike aspect. *Cercidium praecox* is usually rounded or flat-topped, 3 to 4 m tall, the branches spreading. It has very few lateral branches as compared with the other two taxa (fig. 2). *Cercidium sonorae* is a spreading tree 4 to 8 m tall, usually with rather lax branches. A comparison of other characters of these taxa is given in Table 1. Consideration of *C. sonorae* as a hybrid is based upon distribution, morphological intermediacy and variability, ultraviolet absorption patterns in flowers, and low reproductive potential as assessed by pollen stainability and seed set.

Differences in branching habit between the three taxa were determined by noting the number and length of the branchlets in the terminal 25 cm of a branch (fig. 2). *Cercidium sonorae* is intermediate in number of branchlets, but the branchlets are longer than those of either putative parent; this may account for the more lax appearance of the branches in trees of this taxon. In leaflet length, *C. sonorae* bears close resemblance to *C. praecox*, whereas in petiole length (fig. 3), it is close to *C. microphyllum*.

Recently, it has been demonstrated that flowers on herbarium sheets, when exposed to ultraviolet light, indicate absorption and reflection of ultraviolet rays (Horovitz and Cohen, 1972; Eisner et al., 1973). In preliminary studies on the significance of ultraviolet light absorptive and reflective properties to the biology of certain plants, C. E. Jones found that flowers of *Cercidium floridum* and *C. microphyllum* present a different aspect in ultraviolet light than in visible light; subsequent

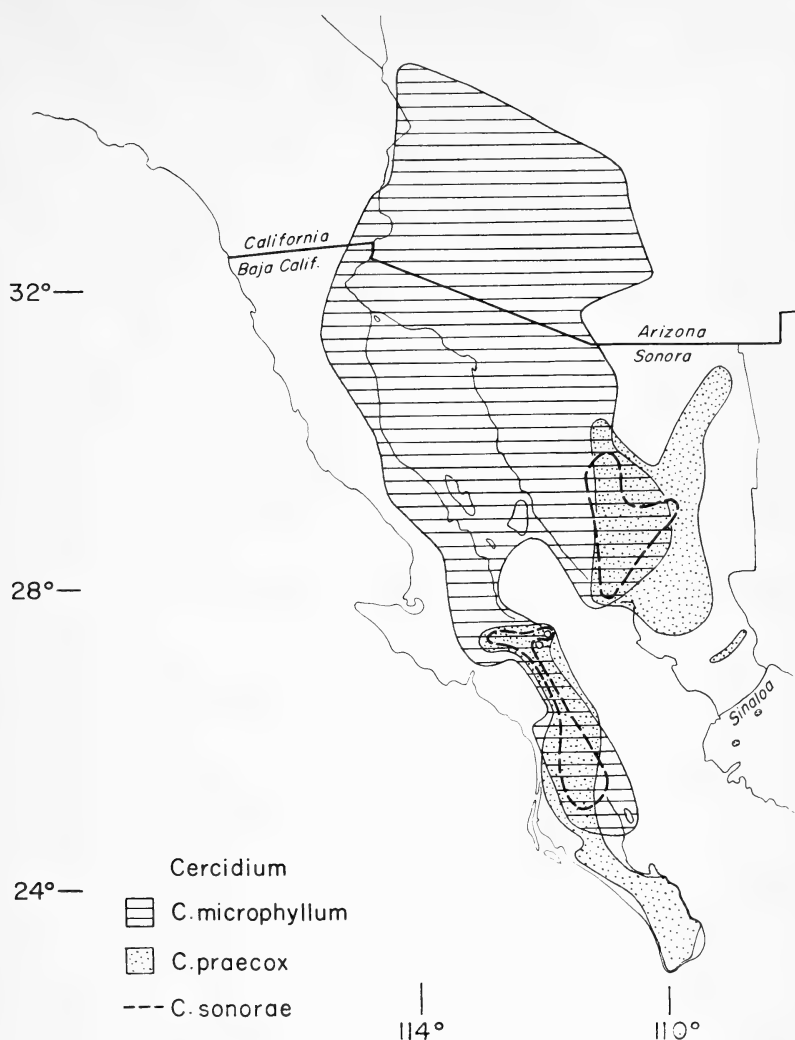


FIG. 1. Distribution of *Cercidium microphyllum*, *C. praecox*, and *C. sonorae* in the Sonoran Desert of northwestern Mexico and southwestern United States. Based on maps by Hastings, Turner, and Warren (1972).

observations indicated that pollinators were highly selective in visiting flowers having one or the other ultraviolet pattern (pers. comm., Jun 1972 and Sep 1973, Calif. State Univ. Fullerton). These observations were made along the lower Colorado River basin (California and Arizona), where the two species are sympatric and reach peak of bloom at approximately the same time and where only a few putative hybrids between these two taxa have been noted.

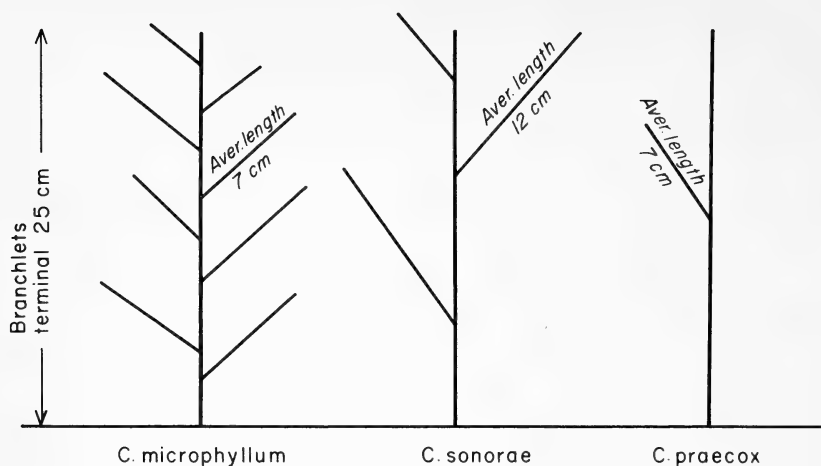


FIG. 2. Diagrammatic representation of the number of branchlets arising in the terminal 25 cm of branches of *Cercidium microphyllum*, *C. sonoreae*, and *C. praecox*.

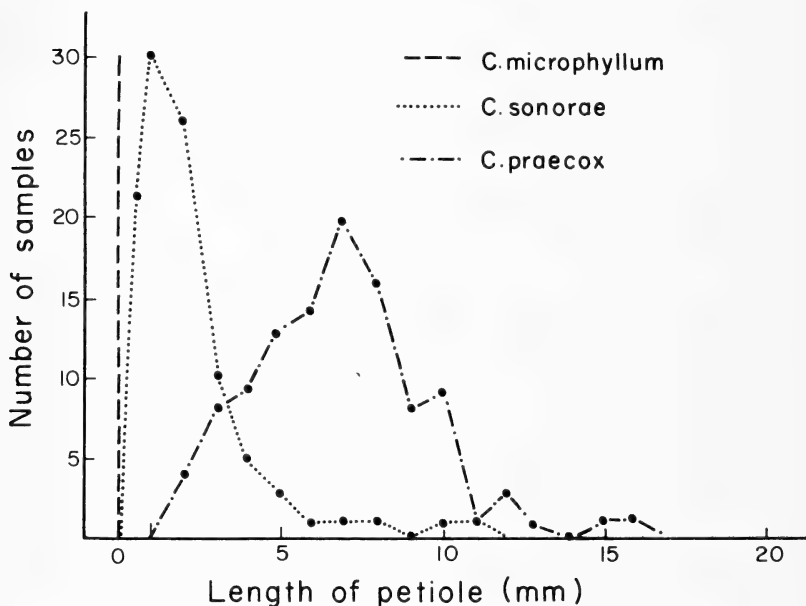


FIG. 3. Comparison of petiole lengths in *Cercidium microphyllum*, *C. sonoreae*, and *C. praecox*.

Herbarium specimens of *Cercidium microphyllum*, *C. praecox*, and *C. sonoreae* were examined under long-wave ultraviolet light to determine if the ultraviolet absorptive and reflective properties support the hypothesis of *C. sonoreae* being of hybrid origin. All specimens examined

TABLE 1. COMPARATIVE CHART INDICATING THE INTERMEDIATE POSITION OF CERCIDIUM SONORAE BETWEEN ITS PUTATIVE PARENTS

CHARACTER SPECIES	<i>Cercidium microphyllum</i> "dipua" "dipuga"	<i>Cercidium sonore</i> "palo estribo"	<i>Cercidium praecox</i> "palo brea"
Branching pattern (terminal 25 cm.)	Many short branchlets, often stout.	A few slender branchlets.	An occasional stout branchlet.
Bark surface	Finely horizontally striate.	Smooth, or obscurely horizontally striate; sometimes with inconspicuous waxy coating.	Quadrangle pustulate and waxy-coated.
color	Yellow-green, lower trunk gray.	Green to yellow-green, lower trunk gray.	Bright green throughout.
Axillary bud scales	Present, but usually not conspicuous.	From inconspicuous to conspicuous.	Abundant, dark, and conspicuous.
Axillary thorns	Lacking, the branchlets spine-tipped.	Present or lacking, slender.	Present, long and stout.
Inflorescence	Open racemes on terminal and sub-terminal branches.	Open racemes on terminal and sub-terminal branches.	Forming sub-sessile appearing clusters along old branches.
Flowers	Clawed upper petal white or creamy-white; other four petals yellow, the limb lanceolate or rhomboidal.	Clawed upper petal varying from creamy to yellow and with or without orange dots; other four petals ovate with pointed apex.	Petals all deep yellow, the upper clawed petal often orange-dotted; limb of other petals broadly ovate.
Legumes	Torulose, strongly tapered apically and basally, longitudinally striate-veined, not papery.	Somewhat constricted between the seeds, conspicuously longitudinally striate-veined, not papery.	Flat and papery, net-veined, not or scarcely constricted between seeds.
Seeds	Sub-globose, brown.	Oblong, mottled.	Oblong, mottled.
Leaflets number of pairs per pinna	Mean: 6.11 pairs Range: 1-13 pairs	Mean: 6.4 pairs Range: 4-12 pairs	Mean: 6.5 pairs Range: 3-13 pairs
length (mm)	Mean: 2.0 Range: 0.5-5.0	Mean: 3.5 Range: 2 - 6	Mean: 5.9 Range: 3 - 8
petiole length (mm)	Sessile	Mean: 2.0 Range: 0-6 (-12)	Mean: 7.6 Range: 3-19
Pollen viability	89 to 99 percent	42 to 76 percent	95 to 96 percent

For each character, the heavy horizontal rule indicates the resemblance of *C. sonore* to the putative parents.

were collected by the author in southern Baja California and in Sonora between 1960 and 1973. Each collection number refers to material from a single tree.

In *Cercidium microphyllum* (nine collections examined), all of the petals absorb ultraviolet light, i.e., the petals appear dark (fig. 4, CEMI), even though the upper petal in this species is white or creamy white under visible light and the other four petals are yellow.

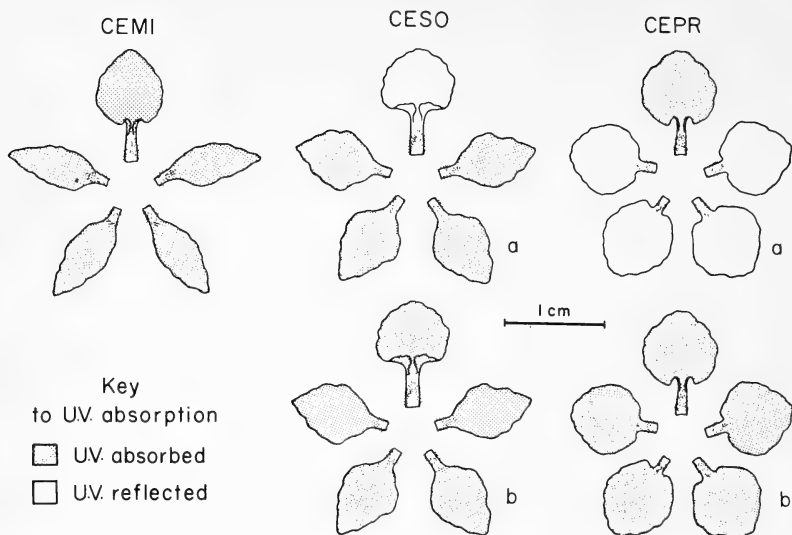


FIG. 4. Patterns of ultraviolet light absorption in flowers of *Cercidium microphyllum* (CEMI), *C. sonore* (CESO), and *C. praecox* (CEPR). Degrees of ultraviolet light absorption (strong or weak) are not differentiated in the diagrams. Differences in petal shape between the three taxa (as noted in Table 1) are also portrayed in the figures. References to *a* and *b* are in text.

Petals of *C. praecox* are all a deep yellow under visible light. In all but two of the ten collections of *C. praecox* examined, the upper petal showed strong absorption of ultraviolet light, i.e., appeared very dark, and the other four petals reflected it, i.e., appeared yellow (fig. 4, CEPR a). In one of the two atypical collections (Carter 4412, between Rancho Segundo Paso and Misión San Javier, ca lat. $25^{\circ}51' N$, long. $111^{\circ}32' W$, Baja California Sur, 21 Apr 1962), five flowers exhibited weak absorption in all five petals (fig. 4, CEPR b). Two other flowers of the same collection showed weak absorption in the upper petal while the other four reflected ultraviolet light, i.e., these flowers approached the preponderant pattern for the taxon. In the other atypical collection of *C. praecox* (Carter, Hastings & Turner 5597, 20 km S of Carbo junction on highway between Hermosillo and Guaymas, Sonora, 3 May 1971), fifteen flowers were of the usual type for this species while one flower exhibited only a slight degree of absorption in the upper petal with the other four being reflective, and a second flower showed slight absorption in all five petals.

In *Cercidium sonore* (14 collections examined), there are two main types of floral pattern under ultraviolet light, one with the upper petal reflective and the balance absorptive (fig. 4, CESO a), and the second with all the petals strongly absorptive (fig. 4, CESO b). In three of the fourteen collections examined both patterns were present in approxi-

mately equal numbers in each of the given trees (*Carter 5669* and *5671*, 55 km E of Villa Insurgentes on highway to Loreto, Baja California Sur, 3 May 1972; *Carter 5672*, base of hills NW of Loreto, Baja California Sur, 5 May 1972). Although Jones found that pollinators were highly selective in relation to different flower patterns in sympatric populations of *C. microphyllum* and *C. floridum*, it appears that such selectivity is not strongly operative in the case of *C. microphyllum*, *C. praecox*, and *C. sonorae*.

Differences in the absorption of ultraviolet light do not appear to be correlated with petal color. In *C. microphyllum* there is strong absorption of ultraviolet light in the upper white or creamy-white petal as well as in the balance of the petals, all of which are yellow. In *C. praecox*, wherein all five petals are deep yellow, the upper petal strongly absorbs and the others reflect ultraviolet light in the majority of cases. In *C. sonorae*, wherein the upper petal varies from nearly white through creamy yellow to yellow (and sometimes even splotched white and yellow), there appears to be no correlation of ultraviolet light absorption with these colors. However, greater stability of the ultraviolet pattern in the putative parents and variability of the pattern in *C. sonorae* lend support to the hypothesis of the hybrid origin of *C. sonorae*.

Unfortunately, ordinary herbarium specimens of *Cercidium* do not lend themselves to statistical studies of ultraviolet light absorption because in each specimen only a few flowers become pressed in such a position that all five petals are clearly displayed. In order to make a definitive study, all of the open flowers in an inflorescence should be spread out and pressed individually and more than one inflorescence per tree should be so prepared. In addition, it should be noted which flowers are pre- and which are post-anthesis in order to determine whether or not the stage of floral development is correlated with the degree of absorption of ultraviolet light. Such an approach might shed some light on the factors determining the absorption and reflection of ultraviolet light in *Cercidium* flowers.

Pollen viability (as indicated by aniline-blue lactophenol staining) is from 89 to 99 percent for *Cercidium microphyllum* and *C. praecox*, but only 42 to 76 percent for *C. sonorae* (Carter and Rem, 1974). Furthermore, field observations have shown that there is often poor seed-set on trees of *C. sonorae*, whereas trees of other species of *Cercidium* in the area evidence good seed-set [pers. comm. Hastings (ARIZ) to Carter, 24 May 1972]. The relatively lower fertility of *C. sonorae* gives strong support to the hypothesis of its hybrid origin.

Study of meiotic chromosomes of *Cercidium sonorae* might further substantiate the hypothesis of a hybrid origin. Unfortunately, the chromosomes of this taxon have yet to be studied. The single report in the literature for *C. sonorae* (Turner and Fearing, 1960) probably is based on misidentified material of *C. praecox* [pers. comm., R. M. Turner

(U.S.G.S., Tucson, Ariz.) to Carter, 23 Jun and 18 Aug 1972]. No voucher was preserved [pers. comm., B. L. Turner (TEX) to Carter, 5 Jul 1972].

From comparison of the several characters as made in figures 2, 3, and 4 and those summarized in Table 1, it can be seen that *Cercidium sonorae* is extremely variable, some of the characters bearing a close resemblance to those of *C. microphyllum* and other characters being like those of *C. praecox*. In still other features, such as the color of the upper petal, the entire gamut of variation between the conditions in the two parents is displayed. The position of the heavy horizontal lines in Table 1 indicates my concept of the resemblance of *C. sonorae* to its putative parents.

In conclusion, I refer to the discussion of hybridization by Stebbins (1950) in which he indicates that interspecific hybridization among higher plants has been shown to be rather common in nature. Most of the examples given, however, are of herbaceous plants. He goes on to say that first and succeeding generations of offspring of most natural hybrids are very likely to represent backcross types rather than true F_2 segregates (ibid, p. 261). The variation in *C. sonorae* may well be interpreted in this light.

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THE BURSERACEAE IN NORTH AMERICA NORTH OF MEXICO

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This paper is based on a study for the Flora North America Program, supported by National Science Foundation Contract C-757 with the Smithsonian Institution. The descriptions of the taxa follow the outline and glossary developed for Flora North America (Porter et al., 1973). Relevant literature for the family in the United States is listed by Brizicky (1962).

BURSERACEAE

Plants deciduous, shrubs or trees, dioecious, older bark peeling off in thin, papery sheets. Leaves imparipinnate, alternate, usually crowded at ends of branches or twigs. Leaflets opposite or subopposite, sessile to petiolulate, entire to irregularly crenulate, glabrous. Petioles alate or not, glabrous to pubescent. Rachises alate or not. Inflorescences axillary or subterminal, racemose, paniculate, glabrous to puberulent, appearing just before or simultaneously with new leaves. Flowers functionally unisexual. Sepals 3 or 5, connate basally, deciduous or persistent, glabrous. Petals 3 or 5, recurved and spreading, glabrous. Stamens 6 or 10. Filaments distinct, free, subulate, insertion at base of disc, glabrous. Anthers smaller and abortive in carpellate flowers. Disc 6- or 10-lobed, glabrous. Ovaries 1, superior, sessile, ovoid, glabrous, lobes 3, locules 3, abortive in staminate flowers. Ovules 2 per locule. Styles 1. Stigmas 1, capitate, lobes 3. Fruits drupes, ellipsoid, ovoid, or subglobose, more or less triangular in cross-section, coriaceous, 5–12 mm long, loculicidal, valves 3, glabrous; pyrenes 1(–2).

A primarily tropical family of about 20 genera and 600 species.

BURSERA Jacq. ex L., Sp. Pl. ed. 2. 471. 1762, nom. cons. [TYPE: *B. simaruba* (L.) Sarg. (*Pistacia simaruba* L.)].

Terebinthus P. Br., Civ. Nat. Hist. Jamaica 345. 1756, non *Terebinthus* P. Mill., Gard. Dict. Abr. ed. 4. 1754.

Simaruba Boehmer in Ludwig, Def. Gen. Pl. ed. 3. 513. 1760.

Elaphrium Jacq., Enum. Syst. Pl. Carib. 3. 1760.

The only genus occurring in North America north of Mexico.

About 100 species in the tropics and subtropics of the Americas. The copious resin of the trunks and branches has been used in making incense.

KEY TO BURSERA IN THE UNITED STATES

Leaves and inflorescences borne on short lateral twigs; leaves 2–11 cm long; petioles to 2 cm long, glabrous.

Leaflets 7–15, lanceolate to ovate or obovate, 15–40 mm long, 3–15 mm wide *B. fagaroides* var. *elongata*

Leaflets 7–35, narrowly oblong, narrowly elliptic, or spatulate, to 5 mm long, to 1 mm wide *B. microphylla*

Leaves and inflorescences borne on main axes; leaves 9–32 cm long; petioles 2.5–8.5 cm long, pubescent to glabrate . . . *B. simaruba*

BURSERA FAGAROIDES (H.B.K.) Engl. var. *ELONGATA* McVaugh & Rzed., Kew Bull. 18:371. 1965 [TYPE: Nayarit, 12 mi SE of Acaponeta, *McVaugh 21752* (MICH)].

B. odorata T. S. Brandeg., Proc. Calif. Acad. Sci., ser. 2, 2:138. 1889. *Terebinthus odorata* (T. S. Brandeg.) Rose, Contr. U. S. Natl. Herb. 10:121. 1906. *Elaphrium odoratum* (T. S. Brandeg.) Rose, N. Amer. Fl. 25: 250. 1911. [TYPE: Baja California, San Gregorio, *Brandeg s. n.* (UC)].

B. tenuifolia Rose, Contr. U. S. Natl. Herb. 3:314. 1895, non *B. tenuifolia* Engl. ex O. Ktze., Rev. Gen. Pl. 1:107. 1891. *Terebinthus tenuifolia* Rose, Contr. U. S. Natl. Herb. 10:122. 1906. *Elaphrium tenuifolium* (Rose) Rose, N. Amer. Fl. 25:252. 1911. [TYPE: Sinaloa, Lodiago, *Palmer 1581* (US)].

Elaphrium covillei Rose, N. Amer. Fl. 25:250. 1911. [TYPE: Sonora, ca 6 mi W of Torres, *Coville 1640* (US)].

B. lonchophylla Sprague & Riley, Kew Bull. 1923:168. 1923 [TYPE: Sinaloa, Cerro del Muerte de Quelele, Tasajera, Choix, *González Ortega 896* (K)].

Plants shrubs or small trees; bark gray-brown. Leaves 5–11 cm long, borne on short lateral twigs. Leaflets 7–15, lanceolate to ovate or obovate, opposite, sessile, 15–40 mm long, 3–15 mm wide, acute to rarely rounded apically, slightly oblique basally, margin irregularly crenulate. Petioles not alate, glabrous. Rachises slightly alate. Inflorescences axillary or subterminal, 1–2-flowered, 2–3 cm long, glabrous, borne on short lateral twigs. Staminate flowers 5-merous. Carpellate flowers 5-merous. Sepals deciduous. Drupes ovoid, 7–9 mm long; pyrenes 1.

In the United States known only from a few populations at ca 1000 m elevation in the mountains of Pima County, Arizona: semiarid limestone cliffs, hillsides, and slopes; flowering July–August. Occurring in like habitats in Mexico at 50–1600 m from Sonora to Guerrero.

BURSERA MICROPHYLLA Gray, Proc. Amer. Acad. Arts 5:155. 1861. *Terebinthus microphylla* (Gray) Rose, Contr. U. S. Natl. Herb. 10:120. 1906. *Elaphrium microphyllum* (Gray) Rose, N. Amer. Fl. 25:250. 1911. [TYPE: Sonora, Sierra Tule, *Schott 1855* (GH)].—Elephant Tree, Torote, Copál.

Plants shrubs or small trees; bark pale grey or white. Leaves 2–3 cm long, borne on short lateral twigs. Leaflets 7–35, narrowly oblong, narrowly elliptic, or spatulate, opposite or subopposite, sessile, to 5 mm long, to 1 mm wide, obtuse apically, margin entire. Petioles narrowly alate, glabrous to rarely pubescent basally. Rachises narrowly alate. Inflorescences subterminal, 1–3-flowered, 5–15 mm long, glabrous, borne on short lateral twigs. Staminate flowers 5-merous. Carpellate flowers 3-merous. Sepals deciduous. Drupes more or less ellipsoid, 5–8 mm long; pyrenes 1.

Locally abundant at low elevations in rocky soils in the Lower Colorado Valley subdivision of the Sonoran Desert in southeastern California and southwestern Arizona; desert canyons, hillsides, and slopes; flowering June–July. Occurring in like habitats in the same subdivision in northeastern Baja California and northwestern Sonora.

BURSERIA SIMARUBA (L.) Sarg., Gard. & Forest 3:260. 1890. *Pistacia simaruba* L., Sp. Pl. 1026. 1753. *Terebinthus brownei* Jacq., Enum. Pl. Carib. 18. 1760, nom. illeg. *B. gummifera* L., Sp. Pl. ed. 2. 471. 1762, nom. illeg. *T. simaruba* (L.) W. F. Wight in Rose, Contr. U. S. Natl. Herb. 10:122. 1906. *Elaphrium simaruba* (L.) Rose, N. Amer. Fl. 25:246. 1911 [TYPE: Jamaica, *Sloane s. n.* (BM.)]—Gumbo Limbo, Almácigo.

Elaphrium ovalifolium Schlecht., Linnaea 17:248. 1843. *B. ovalifolia* (Schlecht.) Engl., Bot. Jahrb. 1:43. 1881. *Terebinthus ovalifolia* (Schlecht.) Rose, Contr. U. S. Natl. Herb. 10:121. 1906. [TYPE: Mexico, *Schiede s. n.* (B)].

Elaphrium integerrimum Tul., Ann. Sci. Natl. Bot., sér. 3, 6:369. 1846. *B. integerrima* (Tul.) Triana & Planch., op cit., sér. 5, 14:303. 1872. [TYPE: Colombia, Alto del Machin, Quindio, *Goudot s. n.* (P)].

Plants trees or shrubs; bark copper-red. Leaves 9–32 cm long, borne on main axes. Leaflets 5–11, broadly ovate to ovate-oblong or obovate, opposite, petiolulate, 27–115 mm long, 15–50 mm wide, acuminate apically, oblique basally, margin entire. Petioles not alate, pubescent to glabrate. Rachises not alate. Inflorescences axillary, many-flowered, 2.5–10 cm long, glabrous to puberulent, borne on main axes. Staminate flowers 5-merous. Carpellate flowers 3-merous. Sepals persistent. Drupes subglobose, 9–12 mm long; pyrenes 1(–2).

Frequent to infrequent in calcareous soils near sea level in southern Florida and the Keys; hammocks and thickets; flowering April–June. Widespread throughout the Caribbean region, occurring from Florida and northeastern Mexico through Central America and the West Indies to Panama, Colombia, and Venezuela.

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NOTES AND NEWS

AN OBSERVATION OF SOME SUGAR PINE RELICTS.—Near the shore of Anne Lake in the Minarets Wilderness Area of the Sierra National Forest, in Madera County, California, at 2,900 m, stands a sugar-pine snag of about 1.5 m diameter at ca 1.4 m above ground level, and about 30 m in height. A companion snag, also sugar pine (*Pinus lambertiana* Dougl.), about half that diameter and about 23 m in height, leans toward the larger snag close by. The strange thing about these snags is that there are no living sugar pines in their vicinity, nor other dead ones. Moreover, the larger of the two has a greater diameter than any tree, living or dead, in its vicinity. The neighbors of the two snags are trees of western white pine (*Pinus monticola* Dougl.), lodgepole pine (*Pinus contorta* Dougl. var. *murrayana* Engelm.), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.). George B. Sudworth (*Forest Trees of the Pacific Slope*, 1908) gives 2,740 m (7,000 ft.) as the maximum elevation for sugar pine in the southern Sierra Nevada, and Willis L. Jepson (*The Trees of California*, second edition, 1923) gives 2,580 m. (8,500 ft.). Moreover, there are no sugar pines along the Fernandez Trail into the Anne Lake vicinity from Clover Meadow, 17.6 km to the southeast at 2,140 m. Anne Lake is shown on the Merced Peak Quadrangle of the U. S. Geological Survey's 15-minute series of topographic maps at Longitude 119°22' W and Latitude 37°36' N.

I identified the snags from bits of bark clinging to the trunks and more bark scattered on the ground around the snags, also from chips of wood cut from the larger snag. The identification of the bark was verified by Prof. Robert A. Cockrell, School of Forestry and Conservation, University of California, Berkeley. A sample of the wood was ground and analyzed by Dr. Arthur Anderson, of the Forest Products Laboratory, University of California (situated in Richmond, near Berkeley). He reported the presence of pinitol, which would suggest that the sample was sugar pine. No old cone parts were in evidence on the ground around the snags.

The two sugar-pine snags are situated among granite outcrops on an east-facing moderate slope on the west side of Anne Lake. Most of their small branches have fallen off. One of the larger snag's several tops has fallen to the ground and is well advanced in rot. This top may have been knocked off by lightning. No galleries of pine beetles were apparent on the weathered wood surface. It is difficult to estimate when the death of these trees occurred, but perhaps in the range of 25 to 50 years—certainly in decades rather than centuries. The larger may have been as much as 400 to 500 years old at death; the smaller, evidently suppressed, may have been about as old.

How does sugar pine happen to have grown at this elevation? We may theorize that this part of the Sierra had a definitely warmer climate several centuries ago, and that sugar pine became established and thrived. Perhaps birds or mammals including man (prehistoric Indians) in some way brought in the sugar-pine seed, which germinated under favorable conditions. The trees then survived during a period sufficiently favorable to grow to maturity.

It was most amazing to find these dead pines (in July 1972) far above the present elevational range of living sugar pines. I would appreciate knowing if others have made similar discoveries. A comparison of the annual rings of the sugar-pine snags with rings of the bristlecone pine (*Pinus aristata* Engelm.), in the White Mountains about 100 km airline to the east, would no doubt serve to date the period when these trees grew.—RICHARD H. MAY, 7 Neila Way, Mill Valley, California 94941.

ALLOTROPA VIRGATA (ERICACEAE), FIRST RECORDS FOR IDAHO AND MONTANA.—*Allotropa virgata* T. & G., a distinctive, red and white candy-striped saprophyte, has been collected from three stations in the Idaho Batholith region of the Northern Rocky Mountains. It was first collected in the Northern Rocky Mountains during 1965 in the Bitterroot Mountains, Ravalli County, Montana, 2 km SE of St. Mary Peak (*Stickney 100B*, Intermountain Forest and Range Experiment Station—Missoula; Sec. 26, T.9N., R.21W., M.P.M.; elev. 2100 m, 1 Aug 1965). First records for Idaho were made in Idaho County during 1972: (1) Selway River Valley ca 1.6 km SW of the Moose Creek Ranger Station (*Habeck 2503*, IFRES—Missoula; NW 1/4 Sec. 14, T.32N., R.12E., B.P.M.; elev. ca 900 m, 13 Jul 1972) and (2) near the summit of the Burgdorf—Warren Road (*Steele 23*, ID, WS, IFRES—Missoula, and IFRES—Boise; NW 1/4 Sec. 19, T.22N., R.6E., B.P.M.; elev. 1900 m, 15 Aug 1972).

Allotropa virgata was previously known from California to British Columbia at low elevations in the Sierra Nevada, Cascade Mountains, and Coast Ranges according to Hitchcock et al. (*Vascular plants of the Pacific Northwest*, Part 4, 1959). It is absent from both Davis' *Flora of Idaho* (1952) and Booth and Wright's *Flora of Montana*, Part 2 (1966). Inquiries to ID, IDS, WS, and MONTU revealed no collections from Idaho or Montana.

The nearest known location for *A. virgata* is the east slope of the Cascade Range (Hitchcock et al., *ibid.*); consequently, the three collections from the Northern Rocky Mountains represent an eastward extension of about 480 km. Within the Northern Rocky Mountains its present known distribution extends approximately 185 km (intervals of 71 and 117 km separate the three stations). On site, this saprophyte appears to be rare. Numbers of plants observed varied from seven to one for the Montana station. In Montana, its occurrence appears to be accidental as it has been looked for since and not found. At one of the Idaho stations, *Steele 23*, *A. virgata* appeared to be substrate specific to decaying wood. Here the total population of seven plants was restricted to the buried margin of a partially-decomposed log. At both sites above 1800 m, *A. virgata* was found growing beneath *Pinus contorta* in the transition between the montane and sub-alpine forest zones. In contrast, at a lower elevation in the Selway River Valley, it was growing in a 250–300 year-old stand of *Abies grandis* and *Thuja plicata*. *Allotropa virgata* may occur in the intervening areas, but small populations, rugged terrain, and remoteness of the region preclude early detection and verification of its distribution in the Northern Rocky Mountains.

The information and material supplied by Dr. James Habeck is gratefully acknowledged.—ROBERT STEELE, Intermountain Forest & Range Experiment Station, Boise, Idaho 83706, and PETER F. STICKNEY, Intermountain Forest & Range Experiment Station, Missoula, Montana 59801.

ARCTOSTAPHYLOS PENINSULARIS IN SOUTHERN CALIFORNIA.—Wells (Madroño 21:268, 1972) recently described *Arctostaphylos peninsularis*, a burl-forming species from above 1200 m in the San Pedro Martir Mountains of Baja California. Recent collections have revealed a similar taxon in southern California (*Keeley 3404*, California State University, San Diego). These plants resemble *A. peninsularis* in the burl-forming habit, glaucous foliage, small closely appressed bracts, and glabrous fruit but differ in having larger leaves with fewer stomata above, longer petioles and pedicels, glandular inflorescences, and larger fruit that tend to split apart.

This taxon seems to be limited in distribution to between 200 and 900 m elevation, from the Santa Margarita Mountains to the Agua Tibia Mountains in northern San Diego and southern Riverside counties. In the middle of its range, from De Luz 30 km east to Pala Creek, this is the only *Arctostaphylos* species found.—JON E. KEELEY, Department of Botany, University of Georgia, Athens 30601.

NOTES ON THE FLORA OF CLATSOP COUNTY, OREGON.—Further exploration of some of the high peaks of the northwestern Oregon Coast Range in Clatsop County allows me to supplement the report I made earlier concerning the floras of Onion Peak and Saddle Mountain (Madroño 22:105–114, 1973). In discussing the characteristic grassy “balds” that occur on these peaks, it was mentioned (p. 107) that Sugarloaf Mountain, a close neighbor to Onion Peak, appeared to have a small “bald” at its summit. On 11 June 1973, I visited Sugarloaf in company with Mr. Dennis Rittenback, of Cannon Beach, and made plant collections and observations specifically to compare its flora with that of Onion Peak and Saddle Mountain. The results confirm the suspected general similarity of species on these rocky and exposed basaltic highlands, including various boreal plants that are at their southern coastal limit of distribution in this region.

Sugarloaf Mountain is a pyramidal peak 871 m in elevation, located 5.4 km north of Onion Peak and 18 km from the ocean. Its apex is a fluted pinnacle of bare rock, about 20 m tall as viewed from the south side; and nestled at the southeast base of this pinnacle is an open, grassy slope of probably no more than 625 m². Prior to logging operations in 1955–56, all the remainder of the peak was densely forested, but today only a few individuals of *Abies amabilis* and *Tsuga heterophylla* remain standing adjacent to the summit “bald” and pinnacle. The “bald” itself is obviously natural, not the result of logging. It occupies a rather gentle gravelly south slope of about 16°, which drops away precipitously to the north and east. The rock comprising this gravelly substrate has a much finer texture than the coarse, hard basalt breccia of the pinnacle itself, suggesting the weathering of a dike like those present on Saddle Mountain. It would be interesting to learn why this tiny area has remained a grassland, resisting colonization by shrubs and trees from the surrounding forest.

The following 34 taxa, found on the gravelly “bald” on Sugarloaf and on ledges and crevices of the basalt pinnacle, are among those most characteristic of similar sites on Onion Peak and Saddle Mountain:

- | | |
|---|--|
| <i>Arenaria rubella</i> (Wallenb.) Smith | <i>Cryptogramma crispa</i> (L.) R. Br. |
| <i>Cerastium arvense</i> L. | var. <i>acrostichoides</i> (R. Br.) Clarke |
| <i>Achillea millefolium</i> L. | <i>Lewisia columbiana</i> (Gray) Robins. |
| <i>Cirsium edule</i> Nutt. | var. <i>rupicola</i> (English) C.L. Hitchc. |
| <i>Erigeron peregrinus</i> (Pursh) Greene | <i>Montia parvifolia</i> (Moc.) Greene |
| ssp. <i>peregrinus</i> | var. <i>flagellaris</i> (Bong.) C.L. Hitchc. |
| <i>Eriophyllum lanatum</i> (Pursh) Forbes | <i>Delphinium menziesii</i> DC. |
| <i>Cardamine pattersonii</i> Henders. | var. <i>pyramidale</i> (Ewan) C.L. Hitchc. |
| <i>Cladothamnus pyrolaeiflorus</i> Bong. | <i>Heuchera micrantha</i> Lindl. |
| <i>Agrostis diegoensis</i> Vasey | <i>Saxifraga bronchialis</i> L. |
| <i>Clamagrostis nutkaensis</i> (Presl) Steud. | var. <i>vespertina</i> (Small) Rosend. |
| <i>Festuca rubra</i> L. | <i>S. mertensiana</i> Bong. |
| <i>Poa gracillima</i> Vasey | <i>S. occidentalis</i> Wats. |
| <i>Romanzoffia sitchensis</i> Bong. | var. <i>latipetiolata</i> C.L. Hitchc. |
| <i>Luzula campestris</i> (L.) DC. | <i>Castilleja hispida</i> Benth. |
| <i>Prunella vulgaris</i> L. | <i>Collinsia parviflora</i> Lindl. |
| <i>Allium crenulatum</i> Wieg. | <i>Nothochelone nemorosa</i> (Lindl.) Straw |
| <i>Stenanthium occidentale</i> Gray | <i>Penstemon cardwellii</i> Howell |
| <i>Epilobium minutum</i> Hook. | <i>Selaginella oregana</i> D.C. Eaton |
| <i>Phlox diffusa</i> Benth. | <i>Lomatium martindalei</i> C.&R. |
| ssp. <i>longistylis</i> Wherry | var. <i>flavum</i> (G.N. Jones) Cronq. |
| | <i>Valeriana scouleri</i> Rydb. |

In this list is a taxonomic correction from my earlier report (*op. cit.*). Dr. C. L. Hitchcock has kindly advised me that the plants referred to as *Saxifraga oregana* Howell are *S. occidentalis* var. *latipetiolata* instead. Also to be added to the flora

of Onion Peak is *Anemone oregana* Gray, which was mistakenly left off the previous list.

Three taxa were found on Sugarloaf Mountain that are known from Onion Peak but have not yet been seen on Saddle Mountain. These are: *Senecio flettii* Wieg., *Saxifraga caespitosa* L. var. *emarginata* (Small) Rosend., and *Castilleja* sp., not yet described.

There were seven species collected on Sugarloaf that I did not find during my explorations of Onion Peak, although it is possible they simply were overlooked: *Linnaea borealis* L., *Carex pachystachya* Cham. ex Steud., *Aira praecox* L., *Festuca bromoides* L., *Poa sandbergii* Vasey, *Trifolium longipes* Nutt. ssp. *caurinum* (Piper) J. M. Gillett, and *Polypodium montense* F. Lang. All of these have been verified from Saddle Mountain except *Linnaea*, but there is no reason to doubt that the latter occurs there also.

Finally, there are two observations to be made on the flora of Saddle Mountain, based on recent collecting activities. *Danthonia californica* Boland. has been found there (*K. L. Chambers 3807*), although I said earlier (*op. cit.*, p. 112) that it was unknown on Saddle Mountain. Also discovered was *Carex macrochaeta* C. A. Meyer (*K. L. Chambers 3741*), a coastal species common from the Aleutian Islands to southern British Columbia. C. V. Piper (*Flora of the State of Washington*, p. 169, 1906) reported this plant from Multnomah Falls, Oregon, but it has not been verified by more recent collections as far as I can determine.—KENTON L. CHAMBERS, Department of Botany, Oregon State University, Corvallis 97331.

A NORTHERN EXTENSION OF THE RANGE OF DARLINGTONIA.—In 1970 we chanced upon a thriving stand of *Darlingtonia californica* Torr. near Sand Lake, Tillamook County, Oregon (T3S, R10W, S 1/2 of SW 1/4 of Sec. 14, just north of the Sand Lake Road). The habitat is a hummocky, slightly sloping bottomland with numerous rivulets and a small stream connecting two sphagnum bogs. The plant community is dominated by a thick stand of scrubby trees [*Thuja plicata* Donn, *Pinus contorta* Dougl., *Picea sitchensis* (Bong.) Carr.]; shrubs, including *Myrica californica* Cham., a typical associate of *Darlingtonia*; and a ground cover of sphagnum and bog phanerogams such as *Drosera rotundifolia* L. and *Vaccinium oxycoccus* L. The *Darlingtonia* grows among the shrubs and sphagnum at the edges of the hummocks and rivulets. Published records of *Darlingtonia* cite its northernmost limit as Lane County, Oregon, although the Oregon State University Herbarium at Corvallis contains a collection from Hidden Lake in Lincoln County, about 21 kilometers north of the Lane County line (OSC 93130, leg. A. N. Steward, 26 December 1953). Our find of *Darlingtonia* in Tillamook County extends its known range some 100 kilometers north of earlier recorded sites. A specimen has been deposited in the Oregon State University Herbarium (OSC 134284).—J. M. TRAPPE, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Corvallis, Oregon 97331, and J. W. GERDEMANN, Department of Plant Pathology, University of Illinois, Urbana, Illinois 61801.

LECTOTYPIFICATIONS FOR WESTERN SENECEONEAE (COMPOSITAE).—*Cacaliopsis nardosmia* (A. Gray) A. Gray var. *glabrata* C. V. Piper, Bull. Torrey Bot. Club 29:222, 1902. [=CACALIOPSIS NARDOSMIA (A. Gray) A. Gray, Proc. Amer. Acad. Arts 19:50, 1883.] Piper stated, "Klickitat County, Suksdorf, 1883 (type in the Gray Herbarium)." Each of two specimens at GH partially fits the protologue. One is labeled, "Adenostyles / Klickitat Co. (Oregon) Wash! / W. Suksdorf, June 1878." This is little more than a scrap and is mounted with a specimen collected by J. Howell dated June 1879. The second specimen (labeled, "Washington Terr. Suksdorf / 1883 / *Cacaliopsis Nardosmia*") is much better, fits the protologue well but for failing to mention Klickitat Co. on the label, and is here designated lectotype.

Prenanthes stricta E. L. Greene, Pittonia 2:21, 1889. [=RAINIERA STRICTA (E. L. Greene) E. L. Greene, Pittonia 3:291, 1898.] Two specimens at ND-G fit the protologue. I designate as lectotype number 48213 in Herbarium Greeneanum (=ND-G 062645).

PSATHYROTES PILIFERA A. Gray, Proc. Amer. Acad. Arts 19:50, 1880. Gray's brief description is followed by "— S. Utah, near Kanab, Mrs. A. P. Thompson, Parry". At GH two specimens of Parry "115" (labeled, "FLORA OF SOUTHERN UTAH, &c." and "Valley of the Virgen near St. George") are mounted on the same sheet with a specimen collected by Mrs. A. P. Thompson (*s.n.*) and labeled, "Kanab, S. Utah". I designate the Thompson collection as lectotype.—JOHN L. STROTHER, Botany-Herbarium, University of California, Berkeley 94720.

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MORPHOLOGICAL CHANGES WITHIN THE CHAPARRAL VEGETATION TYPE AS RELATED TO ELEVATIONAL GRADIENTS

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Changes in vegetation structure with elevation on the lower slopes of the Sierra San Pedro Martir in Baja California have been described recently (Mooney and Harrison, 1972). It was found that at the lowest elevations the vegetation is a low scrub containing a high proportion of succulents. At somewhat higher elevations, this is replaced by a predominantly drought-deciduous scrub, coastal sage, and finally by an evergreen scrub chaparral. The vegetational trends accompanying these changes include an increase in plant density, an increase in the uniformity of heights of the dominant plants, and a change from predominantly drought-deciduous to predominantly evergreen elements. These ecological trends were interpreted in terms of adaptive responses to differences in moisture availability of the habitat.

The objective of the present study was to determine if similar adaptive clines could be identified within a single one of these physiognomically distinct vegetation types in the Sierra San Pedro Martir. In other words, how finely tuned are these adaptive systems?

The vegetation system chosen for study was the evergreen scrub community or chaparral. Samples were taken at three sites at approximately 500 m intervals representing the elevational extent of this type from its lowest representation near 700 m to near its upper reaches at 1800 m. The sites sampled, which were all on north-facing slopes, were all located along the road to the crest of the Sierra San Pedro Martir via the Melling Ranch. The road approximately parallels latitude 31° north. The sites were chosen on the basis of accessibility and a sufficiently uniform slope face to provide a relatively homogeneous sample area.

It can be assumed that soil water availability increases with elevation along this gradient. This follows simply from the fact of increased rainfall and decreasing temperature with elevation and from the characteristic summer drought throughout the gradient. The only climatic data available for this area are for San Telmo, a station located at 175 m elevation, which is below the base of the transect. At San Telmo average annual precipitation is 160 mm, the bulk of which falls in the winter (Hastings, 1964).

At each site 18 to 20 ten-meter line intercept transects were taken by a random walk process from which the average percent cover of each woody species was determined. Each of these species was also scored for a number of morphological traits including presence or absence of such features as spines, strong leaf odor, and fissured bark. Qualitative estimates were made of the degree of leaf pubescence, leaf texture, and predominant leaf angle. Further, the leaves of each species were classified according to size. The average number of growing points per 20 centimeters of terminal branch (5 to 10 branches) were also noted. Finally, the maximum height encountered for each species was scored. All results given are expressed as a percentage of the ground cover that falls into a given class.

The possible functions of many of these traits such as spines, volatiles, and leaf size and texture have been discussed by Parsons (1973). Other traits such as bark characteristics were chosen because they are well-defined morphological traits and it was felt that inferences about their function might be made if clines were identified.

RESULTS AND DISCUSSION

The three sampled sites had virtually identical total shrub cover (Table 1). Further, the heights of the woody plants were all predominantly in the 1 to 2 meter class (Table 2). Despite this general physiognomic similarity the species composition differed among the three stands. *Adenostoma fasciculatum* (chamise) and *Yucca schidigera* (Spanish bayonet) were the only two species encountered at all three sites. Adjacent sites, in each case, had over a third of their species in common. However, when percent cover is considered, the similarity between sites is somewhat less (Table 2).

In spite of the general physiognomic similarity of the various stands, there were a number of morphological features that varied systematically with elevation (Table 2). At the lowest and, presumably, driest site, approximately a quarter of the ground was covered by drought-deciduous shrubs. The evergreen elements became increasingly important with elevation and their leaf sizes larger. Coincident with increasing leaf size, vertically-oriented leaves become more prevalent and the leaves more sclerophytic. All of these trends can be related to the differences in water availability along the elevational gradient. At low elevations, where the drought is most severe, drought avoidance by leaf drop is the most important adaptive mode (Table 2). Where leaves are held only during periods of readily available moisture and relatively cool temperature, carbon gain is maximized with mesophytic leaves that can maintain high photosynthetic rates (Mooney and Dunn, 1970; Harrison et al., 1971). Even if leaf overtemperature (degrees of leaf temperature in excess of air temperature) occurs due to inefficient convective cooling, this may be beneficial, since air temperatures are relatively low during the late winter to early spring growing season. At the low eleva-

TABLE 1. PERCENT COVER OF THE PERENNIAL PLANTS ENCOUNTERED IN TRANSECT.

	Elevation in meters		
	760	1220	1830
<i>Arctostaphylos bicolor</i> (Nutt.) Gray	15.0		
<i>Rhus laurina</i> Nutt. in T. & G.	4.6		
<i>Fraxinus trifoliata</i> (Torr.) Lewis & Epling	4.2		
<i>Cneoridium dumosum</i> (Nutt.) Hook.	3.3		
<i>Arctostaphylos oppositifolia</i> Parry	3.0		
<i>Lotus</i> (cf. <i>scoparius</i>)	19.0		
Unknown shrub	0.8		
<i>Haplopappus propinquus</i> Blake	15.0	0.3	
<i>Eriogonum fasciculatum</i> Benth.	8.1	8.9	
<i>Penstemon antirrhinoides</i> Benth.	1.6	12.5	
<i>Galium</i> sp.	0.8	3.2	
<i>Adenostoma fasciculatum</i> H. & A.	14.0	1.8	8.1
<i>Yucca schidigera</i> Roezl.	0.5	0.8	0.9
<i>Prunus ilicifolia</i> (Nutt.) Walp.		9.6	
<i>Rhamnus crocea</i> Nutt. in T. & G.		5.0	
<i>Adenostoma sparsifolium</i> Torr.		4.9	
<i>Artemisia tridentata</i> Nutt.		1.6	
<i>Ceanothus tomentosus</i> Parry var. <i>olivaceus</i> Jeps.		1.4	
<i>Ceanothus cuneatus</i> (Hook.) Nutt.		1.1	
<i>Arctostaphylos parryana</i> Lemmon var. <i>pinetorum</i> (Roll.) Wies. & Schreib.		20.0	47.0
<i>Garrya</i> sp.		5.5	5.9
<i>Heteromeles arbutifolia</i> M. Roem.		5.3	0.7
<i>Lonicera subspicata</i> H. & A. var. <i>denudata</i> Rehid.		3.1	2.0
<i>Rhus ovata</i> S. Wats.		1.6	4.9
<i>Quercus agrifolia</i> Nee			7.4
<i>Ceanothus leucodermis</i> Greene			3.8
<i>Ceanothus greggii</i> Gray var. <i>perplexans</i> (Trel.) Jeps.			2.0
<i>Rhamnus crocea</i> Nutt. in T. & G. ssp. <i>ilicifolia</i> (Kell.) C. B. Wolf			1.3
<i>Salix</i> sp.			1.1
<i>Opuntia</i> sp.			0.6
<i>Eriodictyon angustifolium</i> Nutt.			0.6
Total % plant cover	89.9	86.6	86.3
Percent stand similarity			
Cover type basis	← 13 →	← 32 →	
Species basis	← 40 →	← 45 →	

tion drought-stressed end of the sclerophyll-gradient, the alternative strategy of being evergreen requires that the leaves be very small in order to avoid high leaf overtemperature during the summer months. During this period evaporative cooling by transpiration is strictly limited by low available moisture.

As summer water stress decreases, at higher elevations, evergreen sclerophylly increases (Table 2). Since photosynthesis can occur all year (Mooney and Dunn, 1970), the advantages of not having to replace an entire leaf crop each year, along with the continuous carbon gain during the summer may offset the advantages of the drought-deciduous

TABLE 2. PERCENT WOODY VEGETATION GROUND COVER AT VARIOUS ELEVATIONS HAVING THE FOLLOWING FEATURES. (In certain instances it was not possible to score a particular species for a given feature. Thus the sum of the percentages of the various features does not always equal the total percent vegetation cover as given in Table 1.)

Feature	Elevation in Meters		
	760	1220	1830
Leaf texture			
Mesophytic	52.9	23.3	6.9
Intermediate	35.9	26.2	14.3
Sclerophytic	0.4	37.0	65.2
Leaf angle			
Vertical	6.3	34.4	56.7
Half vertical	2.9	21.3	7.1
Mixed	75.0	26.6	21.5
Horizontal	1.0	3.2	1.1
Leaf type			
Deciduous	25.7	12.5	0.0
Evergreen			
<26 mm ²	38.0	20.2	9.0
26 – 225 mm ²	3.2	10.7	9.0
226 – 1125 mm ²	23.2	35.3	60.7
1126 – 2025 mm ²	0.0	7.0	7.0
>2026 mm ²	0.0	1.0	0.5
Plant height, meters			
<0.5	0.0	0.0	0.0
0.51 – 1.0	0.9	1.1	2.2
1.01 – 1.5	46.6	13.6	5.6
1.51 – 2.0	6.2	31.6	55.9
>2.0	36.2	40.3	22.7
Growing points/20 cm branch			
1	0.5	0.8	1.6
2 – 10	37.5	29.5	16.0
11 – 20	32.0	47.9	66.8
21 – 30	3.3	0.0	2.0
31 – 100	0.9	8.1	0.0
Leaf pubescence			
None	69.3	64.3	74.7
Medium	19.0	19.0	11.7
Heavy	1.0	3.2	0.0
Leaf odor prevalent	18.3	1.9	2.6
Spiny	0.0	0.0	4.5
Fissured bark	46.1	28.2	10.1

shrubs that have high photosynthetic rates during the cool rainy season.

Leaves become larger and more sclerous as elevation and water availability increases. Cooler temperatures at high elevations reduce the probability of leaf overtemperature. The larger leaves confer a competitive advantage by intercepting more light from smaller, competing plants. They may also be more economical to make since it can be inferred that less stem tissue is needed to display a unit of photosynthetic tissue. With decreasing drought and heat stress, more leaves are main-

tained all year. Thus, there should be an increased advantage in maximizing carbon gain during as long a period as temperatures remain optimal for photosynthesis. The increased sclerophylly may reflect an adaptation to photosynthesis at low leaf water potentials later in the season. This adaptation may also be reflected in the increased emphasis on vertically oriented leaves at higher elevation. This orientation would reduce the radiant heat load on the leaves in the middle of the day when the sun's rays are also vertical. The lower leaf temperatures provided by vertical orientation may be especially important when stomata close during summer drought stress periods and evaporative cooling is nil.

Since upper leaves of such chaparral plants as *Heteromeles arbutifolia* are usually above photosaturation (Harrison, 1971), the vertical orientation probably does not significantly reduce carbon gain. Furthermore, it increases light penetration to lower leaves.

Certain morphological features, such as leaf pubescence and plant spininess, showed no strong changes along the elevational gradient. Other features, such as bark characteristics, leaf odor, and the number of growing points, did show distinctive trends (Table 2), the significance of which can only be speculative until experimental data are available.

The results of this survey indicate that there is considerable sorting of adaptive systems even within the climatic limits that circumscribe a single vegetation type. With additional physiological information, those aspects that relate to water and carbon balance of these systems could be quantitatively assessed to provide a model of fitness for any position along this environmental gradient.

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TAXONOMIC AND NOMENCLATURAL NOTES ON
RHUS INTEGRIFOLIA AND RHUS OVATA
(ANACARDIACEAE)

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Considerable confusion has existed during the past 150 years concerning the correct names and authorities for *Rhus integrifolia* and *Rhus ovata*. This paper is intended as a review of the names that have been applied to these taxa, with the hope of clarifying the situation.

Thomas Nuttall, in Torrey and Gray's (1838) *Flora of North America*, described two new species from southern California: *Styphonia integrifolia* and *Styphonia serrata*. The name *S. integrifolia* was applied to entire-leaved specimens and *S. serrata* to specimens with leaves irregularly repand-serrate. These names persisted in the literature for a number of years (Bentham, 1844; Torrey and Gray, 1856; Nuttall, 1859). Torrey and Gray (1856) included a drawing of *S. serrata* and suggested that it was probably not a distinct species. However, from their collection data and drawing, it is clear that their usage of *S. integrifolia* and *S. serrata* was, in part, based on the yet undescribed *Rhus ovata* S. Wats.

Bentham and Hooker (1862) reduced *Styphonia* to a section of *Rhus*; however, they did not make the combination *Rhus integrifolia*. The combination *Rhus integrifolia* was first published by Brewer and Watson (1876), although they attributed the name to Bentham and Hooker. Brewer and Watson, based on specimens collected by Palmer and Wheeler, included western Arizona as part of the range of *R. integrifolia*. I have seen some of those specimens (Palmer 36, MO! GH!), and they proved to be *Rhus ovata*. Again, the name *Rhus integrifolia* was, in part, misapplied. Rothrock (1878) also made the combination *Rhus integrifolia* and he too attributed the name to Bentham and Hooker. Rothrock's *Rhus integrifolia* has been cited by many authors (Barkley, 1937; Shreve and Wiggins, 1964; Raven and Thompson, 1966; Thorne, 1967) as being the first usage of this combination, even though Brewer and Watson preceded Rothrock by two years. Apparently, only Greene (1888) was aware of Brewer and Watson's combination. However, Rothrock based his circumscription of *R. integrifolia* in part on specimens (which he had not seen) collected from Arizona, an area where *R. integrifolia* does not occur. Rothrock's description and knowledge that the specimens (none was cited) were collected in Arizona indicate that he was probably referring to *Rhus ovata*.

The name *Rhus integrifolia*, with an assortment of authorities, appeared in the literature a number of times from 1878 to 1883, and most authors recognized that *Styphonia serrata* was not a distinct species, since entire and serrate leaves can occur on a single bush of *R. integri-*

folia. However, Engler (1883) recognized *Rhus integrifolia*, *R. integrifolia* var. *serrata*, and *R. hindsiana* citing himself as author in all three cases. Engler's *R. integrifolia* included that of Torrey and Gray (1856) and his description (p. 388) was based in part on *R. ovata*. Because of this and noting that a specimen from Baja California (*Hinds s.n.*, K!), which is actually *R. integrifolia* was so different, Engler named it *Rhus hindsiana*. Engler, apparently feeling that specimens of *R. integrifolia* with serrate leaves should be formally recognized, also created *R. integrifolia* var. *serrata* (*Lobb s.n.*, K!). Fortunately, it has not been recognized since. Finally, Watson (1885) recognized and named *Rhus ovata* as a separate entity from *R. integrifolia*, although his description of it as having yellow petals was erroneous and probably due to his use of dried herbarium specimens.

Barkley (1937) described *Rhus ovata* var. *traskiae* (*Trask s.n.*, MO!) and *Rhus integrifolia* var. *cedrosensis* (*Rose 16134*, NY!). Munz (1959) included *R. ovata* var. *traskiae* as a synonym of *R. ovata*. *Rhus ovata* var. *traskiae* is clearly intermediate between *R. ovata* and *R. integrifolia* and is a hybrid between the two species (Young, 1974). *Rhus integrifolia* var. *cedrosensis* appears to be a hybrid between *R. integrifolia* and *Rhus lentii* Kellogg (Young, unpubl. data).

Both taxa have been placed in other genera by various authors. Kuntze (1891) transferred almost all of the then described species of *Rhus* to *Toxicodendron* (*T. integrifolium* and *T. hindsianum*), although he neglected to include the newly described *R. ovata*. *Rhus integrifolia* and *R. ovata* are clearly not members of *Toxicodendron*, at least in the modern concept of the latter genus (see Gillis, 1971). Shafer (1908), apparently feeling that Nuttall's *Styphonia* was distinct from *Rhus*, erected the genus *Neostyphonia*, indicating that *Styphonia* had been used in 1791 by Medicus for a genus of Lamiaceae. Shafer included only *N. integrifolia*; however, Abrams (1910) added *N. ovata*. Few authors have recognized *Neostyphonia* (Abrams, 1917; Millspaugh and Nuttall, 1923), and Barkley (1937), in his monograph of North American *Rhus*, placed *Neostyphonia* in synonymy with *Rhus*. It should be noted that Barkley indicated that *Styphonia* was a new section of *Rhus* citing himself as author. However, Bentham and Hooker (1862) clearly designated *Styphonia* as a section of *Rhus* and should be cited as the authorities for that usage. Later, Barkley (1940) elevated the subgenus *Schmaltzia* to the generic level, so that *R. integrifolia* and *R. ovata* became *Schmaltzia integrifolia* and *Schmaltzia ovata*. Brizicky (1963) has adequately discussed the fact that *Schmaltzia* is a *nomen provisorium* and that the valid name of *Schmaltzia*, if it is separated from *Rhus*, is *Lobadium*. Barkley (1965) later acknowledged this fact. I am currently investigating the Mexican species of *Rhus* subgenus *Lobadium* and at this time feel that there are insufficient data available to warrant the removal of *Lobadium* from *Rhus*.

The following lists of synonymies for *R. integrifolia* and *R. ovata* are presented to summarize and further clarify the nomenclatural situation concerning these two taxa.

RHUS INTEGRIFOLIA (Nutt. in T. & G.) Brewer & Watson, Bot. of Calif. 1:110. 1876.—*Styphonia integrifolia* Nutt. in T. & G., Flora N. Amer. 1:220. 1838.—*Toxicodendron integrifolium* (Nutt. in T. & G.) Kuntze, Rev. Gen. Pl. 1:154. 1891.—*Neostyphonia integrifolia* (Nutt. in T. & G.) Shafer in Britt., N. Amer. Trees. 612. 1907.—*Schmaltzia integrifolia* (Nutt. in T. & G.) Barkley, Amer. Midl. Naturalist 24:650. 1940.—TYPE: San Diego, *Nuttall s.n.* (BM!, photo RSA!). Barkley (1937) indicated that the type of *R. integrifolia* was at GH. However, as recently discussed by Rollins (1972), most of Nuttall's herbarium is located at BM, and the specimens there were not examined by Barkley. The specimen at GH, marked as the type of *R. integrifolia* by Barkley, is at best an isotype. Although Brewer and Watson included *R. ovata* as part of their *R. integrifolia*, they did list *Styphonia integrifolia* as a synonym for their name, so that their *R. integrifolia* was based on the *S. integrifolia* of Nuttall. In accordance with Recommendation 46C of the *International Code of Botanical Nomenclature* (Stafleu, 1972) I have elected not to include Bentham and Hooker as authorities in the citation of the combination *Rhus integrifolia*.

Styphonia serrata Nutt. in T. & G., Flora N. Amer. 1:220. 1838.—*Rhus integrifolia* var. *serrata* (Nutt. in T. & G.) Engler in DC., Monogr. Phaner. 4:388. 1883.—TYPE: San Diego, *Nuttall s.n.* (BM!). Since Engler's *R. integrifolia* var. *serrata* was based on Nuttall's *Styphonia serrata*, its type must be that of *S. serrata* at BM and not, as indicated by Engler, a specimen at K.

Rhus hindsiana Engler in DC., Monogr. Phaner. 4:388. 1884.—*Toxicodendron hindsianum* (Engler) Kuntze, Rev. Gen. Pl. 1:154. 1891.—TYPE: San Quentin, Baja California, Mexico, *Hinds s.n.* (K!).

RHUS OVATA Watson, Proc. Amer. Acad. Arts 20:358. 1885.—*Neostyphonia ovata* (Wats.) Abrams, Bull. New York Bot. Gard. 6:403. 1910.—*Schmaltzia ovata* (Wats.) Barkley, Amer. Midl. Naturalist 24:651. 1940.—TYPE: San Diego Mtns., *Orcutt s.n.*, May 1883 (GH!, photo RSA!).

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HYBRIDIZATION BETWEEN QUERCUS AGRIFOLIA AND Q. WISLIZENII (FAGACEAE)

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Quercus agrifolia Née and *Q. wislizenii* A. DC., are evergreen black oaks with a number of morphological similarities. However, they can be readily distinguished from each other by the differences in timing of acorn maturation. *Quercus agrifolia* acorns mature in one year, while acorns of *Q. wislizenii* require two years. Their ranges are fairly distinct in much of northern California, with *Q. wislizenii* generally occupying more xeric inland areas surrounding the Sacramento and San Joaquin valleys and *Q. agrifolia* confined more to mesic coastal areas.

Hybrids between species of California black oaks have long been recognized. The well known *Q. × morehus* Kell. was shown to be a hybrid between *Q. kelloggii* Newb. and *Q. wislizenii* (Wolf, 1938). The hybrid between *Q. kelloggii* and *Q. agrifolia* var. *oxyadenia* (Torr.) J. T. Howell has been described from San Diego County (Wolf, 1944) and is called *Quercus × ganderi* C. B. Wolf. Finally, the hybrid between *Q. kelloggii* and *Q. agrifolia* has been described from Santa Clara County (McMinn et al., 1949). Hybridization between *Q. wislizenii* and *Q. agrifolia* has not previously been reported.

On the northwest side of Mount Diablo (Contra Costa County, California), in a population apparently made up of *Q. agrifolia*, some trees have characters that make it difficult to key them either to *Q. wislizenii* or to *Q. agrifolia*. One tree in particular is strikingly different from the other oaks in the area and appears to be intermediate between *Q. agrifolia* and *Q. wislizenii*. These observations suggest the possibility that hybridization has occurred between these two species in this area where their ranges overlap.

The purpose of this study was to determine whether or not hybridization has occurred between *Q. agrifolia* and *Q. wislizenii*.

METHODS AND MATERIALS

Populations to be sampled were chosen from within the range of *Q. agrifolia*, from within the range of *Q. wislizenii*, and from areas where the two are sympatric (see Table 1). The number of trees sampled in each area varied; quantities were sampled that were thought to be large enough to demonstrate the pattern of variation within the respective

TABLE 1. SITE NAMES, NUMBER OF TREES SAMPLED, AND LOCATIONS OF SITES FOR POPULATION SAMPLES.

A. Sites within the range of *Q. agrifolia*. *Lafayette* (10): Contra Costa County; 1.61 km SE of Lafayette, near St. Mary's Road. *Fish Ranch Road* (10): Contra Costa County; 3.22 km W of Orinda, at intersection of Fish Ranch Road and highway 24.

B. Sites within the range of *Q. wislizenii*. *Redding* (10): Shasta County; 4.8 km SE of Redding; 1.61 km E of Int. 5. *Vasco Road I* (1): Contra Costa County; 8.1 km N of Int. 580; 0.56 km W of Vasco Road. *Napa* (3): Napa County; 16.4 km N of St. Helena, 0.8 km SE of Aetna Springs. *Deer Valley Road* (18): Contra Costa County; 9.7 km SW of Brentwood; 0.32 km S of intersection of Deer Valley and Marsh Creek Roads.

C. Sites within the zone of overlap of the ranges of the two species. *Donner Canyon* (17): Contra Costa County; 1.61 km to 3.22 km NW of summit of Mount Diablo, between Deer Flat and Donner Canyon. *Junction Camp* (19): Contra Costa County; Mount Diablo, at the intersection of North Gate and South Gate roads, at Junction Camp. *Vasco Road II* (16): Contra Costa County; 11.6 km S of intersection of Vasco Road and Camino Diablo (2.25 km N of Vasco Road I collection). *Benicia* (26): Solano County; 8.1 km NW of Benicia; 60 m W of highway 21.

populations. Only trees with a trunk diameter greater than 11.15 cm at breast height were sampled. No attempt was made to restrict the sampling to a particular type of habitat; in fact, in some instances populations sampled extended through two or more areas that were quite distinguishable ecologically.

Twigs representing at least two seasons' growth were collected from each tree during the period from April to October, 1971. The twigs were taken from the outside of the canopy from 1.5 to 2.7 m from ground level and were collected from four sides of the tree, representing four points separated from one another by ninety degrees. The entire collection of twigs and leaves was sampled systematically, with no opportunity presented for choosing a particular leaf because it seemed more "typical" than others.

Thirteen characters were studied (Table 2). Scatter diagrams were constructed and hybrid indices were calculated for each tree. Hybrid indices were plotted on histograms so that frequency distribution of trees with given index values could be read. Also, a graphical method was used to compare populations by utilizing the mean hybrid number and the mean hybrid index for each population (Gay, 1960). This method of portraying populations has the advantage of showing the nature of the intermediacy a population has. That is, placement of the population on the graph is proportional to the number of hybrid, backcross, and parental types contained in it.

RESULTS

The ten study populations (Table 1) are usefully subdivided into three groups. The first group comprises specimens collected entirely

TABLE 2. CHARACTERS DETERMINED FOR EACH LEAF OF A SAMPLE.

1. Length of leaf blade
2. Length of petiole
3. Width of leaf blade
4. Distance from base of leaf to widest point of leaf
5. Presence or absence of axillary hairs
6. Leaf blade convex or plane
7. Color of abaxial surface of leaf
8. Color of adaxial surface of leaf
9. Number of secondary veins on a side of the leaf midvein
10. Angle of secondary veins to the midvein of leaf
11. Leaf secondary veins parallel or not so
12. Veins pronounced above abaxial surface of leaf or not so
13. Relative size of vein islets in leaf

from within the range of *Q. agrifolia* ("A" in Table 1). The second group is made up of specimens collected from within the range of *Q. wislizenii* ("B" in Table 1). The remaining group comprises four populations from areas of sympatry between the two species ("C" in Table 1); it was not known if any character could consistently be used to separate these populations from either "A" or "B" above.

Seven of the thirteen characters that were examined can be used consistently to distinguish between the *Q. agrifolia* (A) and the *Q. wislizenii* (B) populations (Table 3), but generally they cannot be used to identify or distinguish any of the other four populations as one or the other of the two species.

Three of the seven characters that may be used are quantitative. A good separation can be made between *Q. agrifolia* and *Q. wislizenii* populations by use of the ratio of leaf width to leaf length. This measure of leaf shape shows that leaves of *Q. agrifolia* have a strong tendency to be oval, with the width over half the length. By contrast, the leaves of *Q. wislizenii* have a tendency to be oblong, or two to three times longer than wide. The angle between the lateral veins and the midvein and the number of lateral veins are distinctly different for standard *Q. agrifolia* and standard *Q. wislizenii*. There is a definite tendency for the Donner Canyon, Junction Camp, Vasco Road II, and Benicia populations to show intermediacy and a wider range of values for these quantitative measures.

The remaining four characters, presence of axillary hairs, relative size of vein islets, leaf underside color, and leaf convexity, are qualitative and show a remarkable consistency in separating the parental populations of the two species. Leaves of *Q. agrifolia* show a marked tendency to be convex and dull green on the abaxial surface. They have small vein islets when viewed through a hand lens or microscope, and have tufts of brownish, stellate trichomes in the axils of the major veins. On the other hand, leaves of *Q. wislizenii* exhibit a strong tendency to be plane, to be yellowish green on the abaxial surface, to have relatively large vein islets, and to be glabrous.

TABLE 3. MORPHOLOGICAL CHARACTERS AND CODE TO SYMBOLS USED IN PREPARING SCATTER DIAGRAMS.

	<u>Q. wislizenii</u>	Intermediate	<u>Q. agrifolia</u>
Hybrid Index	0	1	2
Ratio of leaf width to length	.38 - .53	.53 - .58	.58 - .79
	(ordinate of scatter diagram)		
Angle of lateral vein to midvein	42.1° - 65.7°	39.1° - 42°	26.5° - 39°
	(abscissa of scatter diagram)		
Presence of axillary hairs	absent	not scored	present
Symbol	○		●
Number of lateral veins	7.01 - 10.0	6.01 - 7.0	4.0 - 6.0
Symbol	○	●	●
Relative size of vein islets	large	intermediate	small
Symbol	○	●	●
Color of leaf underside	yellow green	not scored	dull green
Symbol	○		●
Convexity of leaf	plane	intermediate	convex
Symbol	○	●	●

Populations were analyzed for evidence of hybridization through construction of pictorialized scatter diagrams and hybrid index histograms. The seven characters outlined above were used in the analyses. Hybrid index scores for each characteristic and symbols used in constructing pictorialized scatter diagrams are listed in Table 3.

Figure 1 is a pictorialized scatter diagram of 52 specimens representing the standard populations of the two species. A pronounced negative correlation exists between leaf shape and lateral vein angle when both species are shown together. When all seven characters are considered

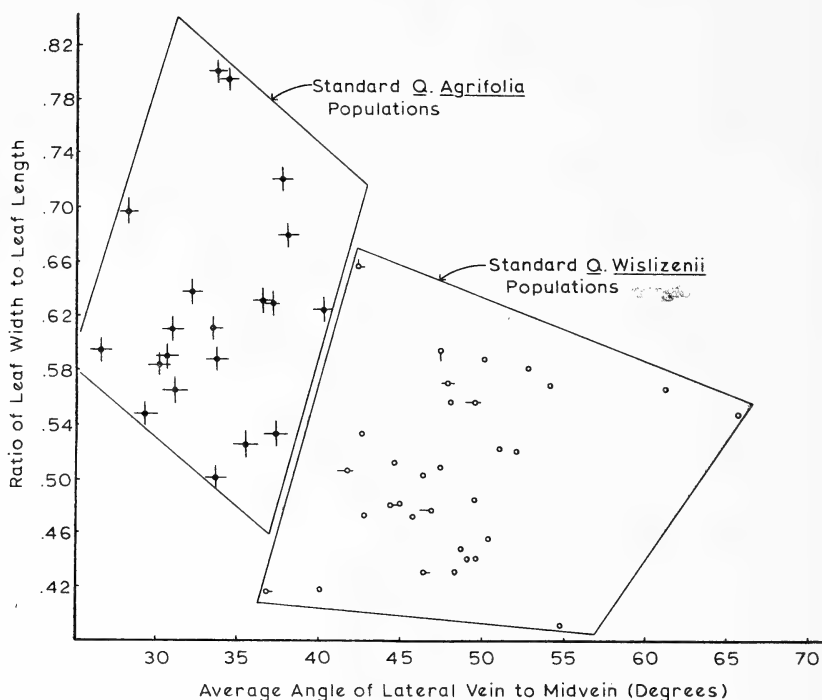


FIG. 1. Pictorialized scatter diagram of fifty-two specimens representing populations of *Q. agrifolia* and *Q. wislizenii*. Each four-sided figure includes representatives of one species. (See Table 3 for code to symbols.)

simultaneously, clear differentiation is evident between *Q. agrifolia* and *Q. wislizenii* (fig. 1).

Approximately five of the seventeen specimens from the Donner Canyon site represent standard *Q. agrifolia* or *Q. wislizenii* individuals; the remaining twelve appear to be intermediate in two or more characters (fig. 2). The result is a close fit to what Anderson (1949) called the recombination spindle, i.e., there is a tendency toward correlation among the variables, but there is no absolute correlation between any of them. The observed variation is best explained by a hybridization hypothesis.

A negative correlation exists between the characters diagrammed from the Junction Camp population (fig. 3). Few standard combinations are in evidence, and a preponderance of intermediate individuals occupy a recombination spindle, which extends from the upper left to the lower right corner of the graph. Further, a loose correlation exists among the characters, and the graph shows a tendency for most recombinants to be in the direction of *Q. agrifolia*.

The recombination spindle for the Vasco Road II population (fig. 4) is a much better fit to the ideal spindle proposed by Anderson (1949) than are the populations diagrammed in figures 2 and 3. While a full

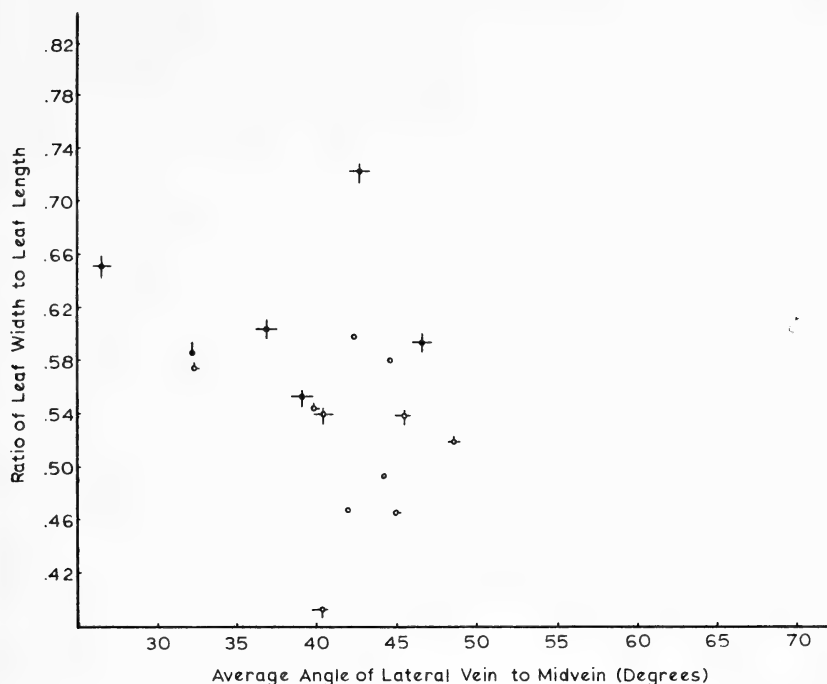


FIG. 2. Pictorialized scatter diagram of specimens from the Donner Canyon population. (See Table 3 for code to symbols.)

range of intermediates appears to exist, no individual is exactly intermediate between the two hypothetical parental combinations.

A somewhat different situation can be seen in the Benicia population (fig. 5). Here the characters of the two parental species appear to be combined and recombined more or less at random. No recombination spindle is evident as in the previous diagrams. On the other hand, there does not appear to be a single specimen that could be called a pure parental combination, though a number of them approach *Q. agrifolia*.

Figures 6A and 6B are hybrid index frequency distributions (Anderson, 1949) for *Q. agrifolia* and *Q. wislizenii* respectively. They illustrate in a more graphic way the complete separation that exists between populations of *Q. agrifolia* and those of *Q. wislizenii*, when the previously mentioned seven characters are used. The *Q. wislizenii* populations differ from those of *Q. agrifolia* chiefly in that five individuals in the former and only one in the latter populations depart from the standard parental combinations by a score of three or more.

In the four intermediate populations (fig. 6C), only 28 percent of the specimens have extreme index scores of 0 to 2 or of 12 to 14, while 72 percent have intermediate scores of from 3 through 11. On the other hand, 59 percent have scores of 8 or more, 33 percent score 6 or less, and 8 per-

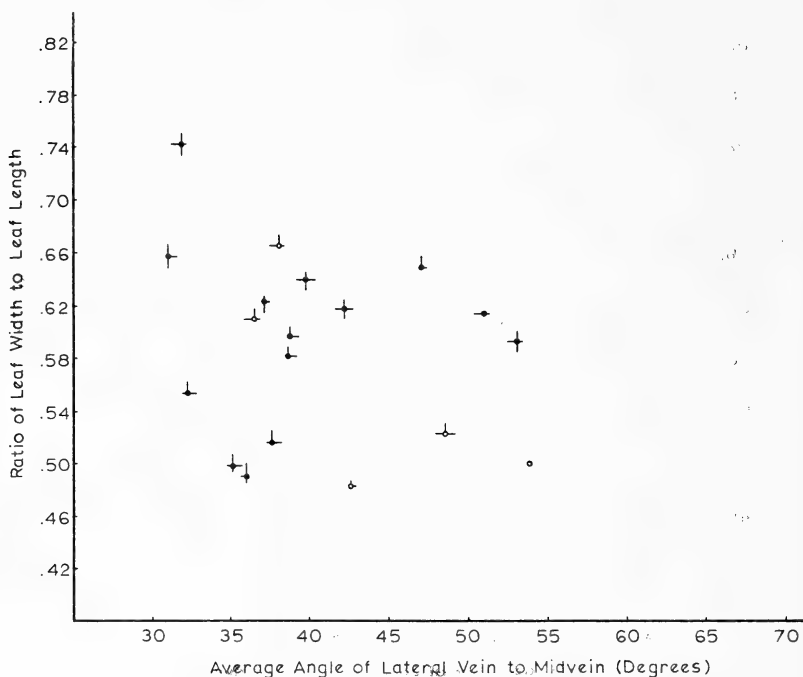


FIG. 3. Pictorialized scatter diagram of specimens from the Junction Camp population. (See Table 3 for code to symbols.)

cent have a score of 7. This indicates a preponderance of specimens with characters tending toward *Q. agrifolia*, and 8 percent of the specimens with a score that indicates the F_1 hybrid condition.

A newer method of comparing populations that contain hybrids has been outlined by Gay (1960). This method combines Anderson's index with a variable called the hybrid number. The hybrid number represents "... the deviation of the hybrid index of the specimen from the nearer of the two extreme values of the hybrid index scale." Figure 7 is a graph of the mean hybrid number against the mean hybrid index for the populations studied. A hypothetical population of *Q. agrifolia* would lie at the lower right corner of the triangle, a population of *Q. wislizenii* at the lower left corner, and a hypothetical population of F_1 hybrids would lie at the upper point of the triangle.

From Figure 7 it is evident that no population sample is made up of pure hybrids; the Benicia population is closest in this respect. Also, of the four intermediate populations sampled, this population is most similar to *Q. agrifolia*; the Junction Camp sample is second in this respect. The degree of this similarity is read by the distance from the side of the triangle connecting the pure hybrid state and the point of the triangle representing *Q. agrifolia*. With this in mind, it can be seen that the Don-

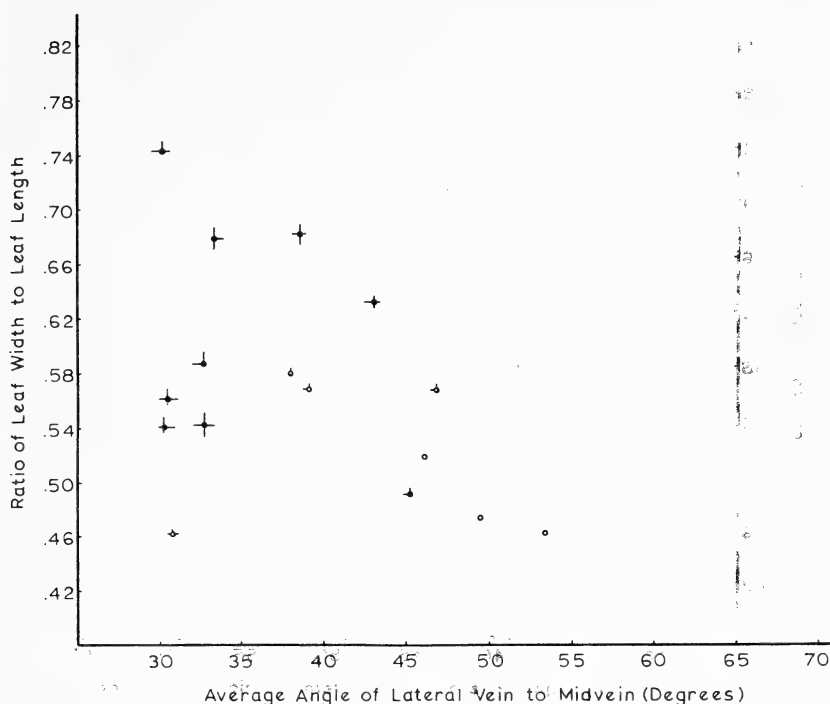


FIG. 4. Pictorialized scatter diagram of specimens from the Vasco Road II population. (See Table 3 for code to symbols.)

ner Canyon (J) and Vasco Road II (N) populations show approximately the same degree of similarity to *Q. agrifolia* as to *Q. wislizenii*. A population made up of equal numbers of the two parental species, but containing no hybrids, would be at midpoint on the abscissa of the graph. A mixture containing equal numbers of *Q. agrifolia*, *Q. wislizenii*, and F_1 hybrids would appear at the "x" locus of the graph. The Vasco Road II sample would appear to be very close in this regard, with the other three intermediate samples showing increasing degrees of hybridity.

One putative hybrid, located at Junction Camp on Mount Diablo, has a hybrid index value of 9, which indicates that it is of a hybrid nature, with slightly more characteristics of *Q. agrifolia* than of *Q. wislizenii*. The leaves are extremely large, unlobed, and with little or no convexity. Hairs are present in the axils of the leaves and the abaxial surface is yellow-green. The foliage is much less dense than in the surrounding trees, which are predominantly *Q. agrifolia*. In May, 1971, at least two acorns were green, nearly full-sized, and growing on twigs produced the previous season. Other, smaller fruits, representing the current season's pollinated flowers also were present. Thus there were present acorns that represented biennial maturation of the fruit, a trait that is characteristic

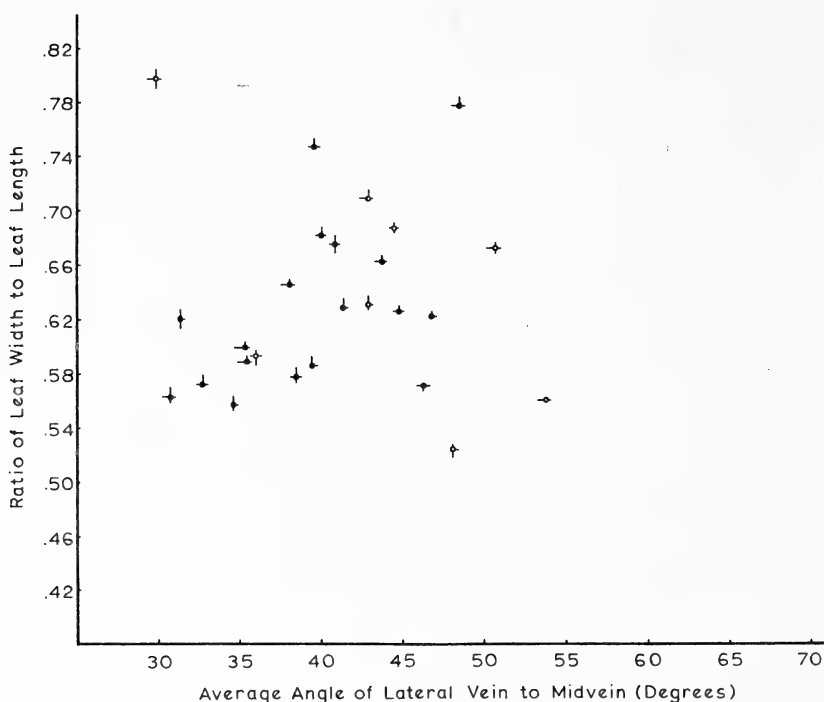


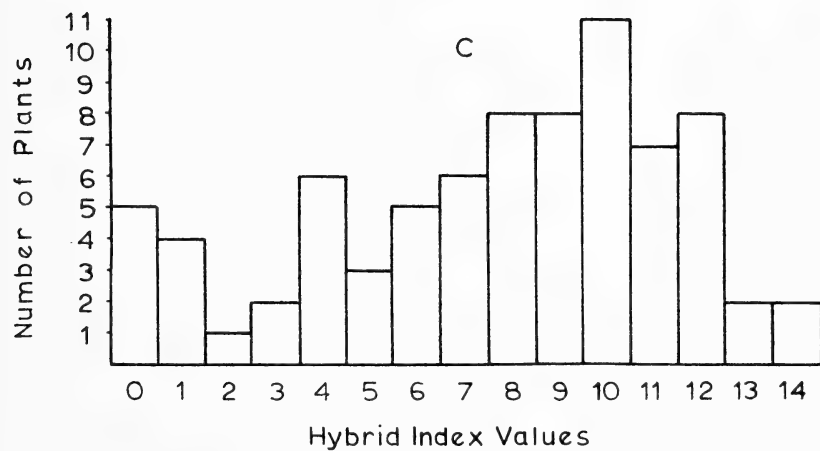
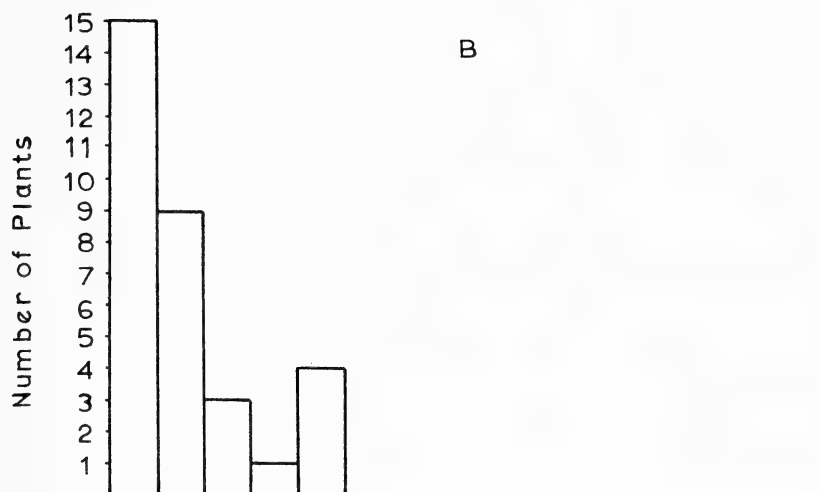
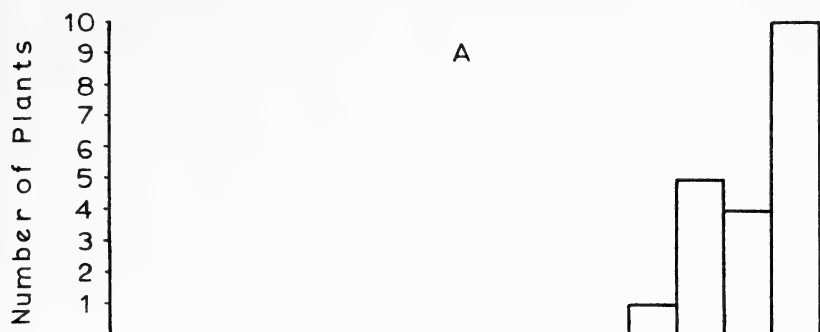
FIG. 5. Pictorialized scatter diagram for specimens from the Benicia population. (See Table 3 for code to symbols.)

of *Q. wislizenii*. Fruiting characteristics of the latter species were combined with vegetative characteristics of *Q. agrifolia* on the same tree.

In July, 1971, acorns present on *Q. agrifolia* growing in the same area were still extremely small and undeveloped, since they do not normally mature until September. The *Q. agrifolia* acorns differed from those of the putative hybrid tree in that they were all of one size class and would mature in a single season. The only other evidence of reproductive activity on the putative hybrid were ten to fifteen abortive fruits, which dropped easily from the tree when touched, and consisted of nothing more than an enlarged involucre.

In contrast to this tree, one that combined leaf characters of *Q. wislizenii* with fruiting characteristics of *Q. agrifolia* was observed in Solano County. This tree has a hybrid index value of 4, which indicates definite *Q. wislizenii* affinities. In September, 1971, mature acorns were present on the then current season's vegetative growth, an important characteristic of *Q. agrifolia*. The Benicia specimen also had an abundance of acorns in 1971, in marked contrast to the putative hybrid of the Junction Camp population.

FIG. 6. Hybrid index frequency distributions. A, Standard populations of *Quercus agrifolia*. B, Standard populations of *Q. wislizenii*. C, Four intermediate populations.



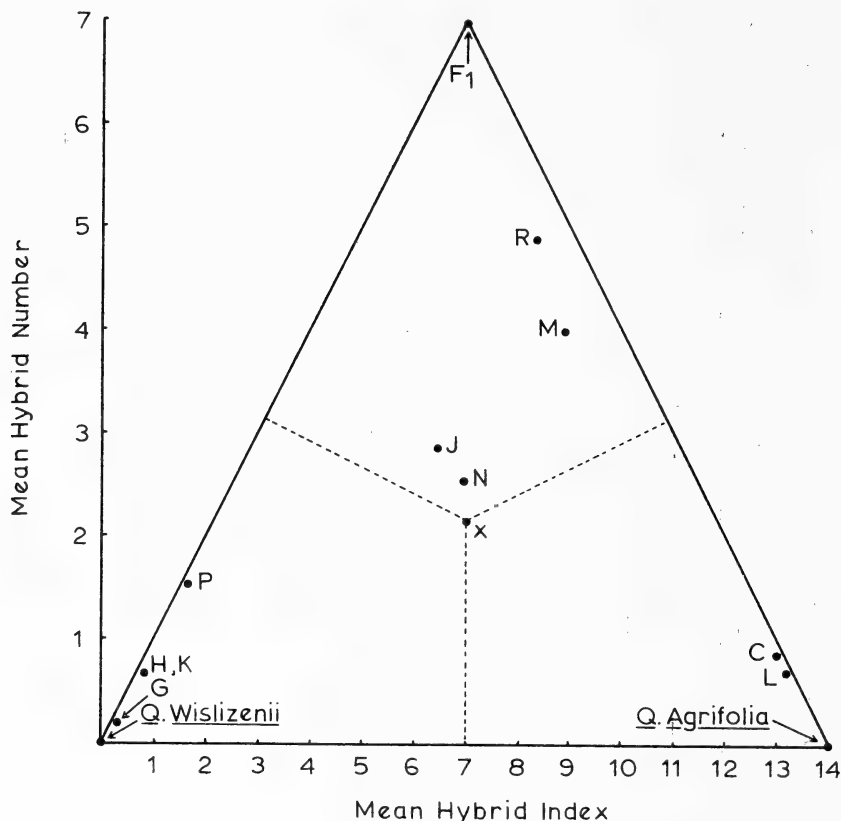


FIG. 7. Relationship between hybrid number and hybrid index for ten actual populations and one hypothetical population (F_1) made up of intermediate F_1 hybrids. Each point on the graph represents a particular population: C—Lafayette; G—Redding; H—Vasco Road I; J—Donner Canyon; K—Napa; L—Fish Ranch Road; M—Junction Camp; N—Vasco Road II; P—Deer Valley Road; R—Benicia.

DISCUSSION

Quercus agrifolia and *Q. wislizenii* long have been thought to be separated both by ecological barriers and by the differences in pollen tube growth (Benson, 1962). Although it is clear from our data that these two species of black oaks are distinct, it is equally clear from the variation patterns of the Donner Canyon, Junction Camp, Vasco Road II, and Benicia populations that hybridization has occurred between them. However, the patterns of variation are not the same for all four populations.

As mentioned previously, the recombination spindles characteristic of the Donner Canyon, Junction Camp, and Vasco Road II populations are evidence that the linkage groups inherited through hybridization in these populations still have a tendency to hold together, though not in

an absolute sense. In the Benicia population (fig. 5), however, the various characters of the two species have combined and recombined more or less at random. A recombination spindle, present in figures 2, 3, and 4, is not present in the diagram for this population.

The same kind of situation was encountered by Tucker (1952) in his study of the evolution of *Q. alvordiana*, in which "... the scatter diagrams conform only in a rather indistinct fashion to the 'recombination spindle' ... and the parental characters are thoroughly 'shuffled' and recombined." He postulates two causes for this situation. First, the character differences between the parents may be determined by a smaller number of genes than Anderson has assumed generally to be the case. Second, the number of generations of interbreeding may be very large.

Either hypothesis is perhaps applicable in Tucker's study, where recombination spindles generally are lacking. In the present study, however, the hypothesis involving a small number of genes is not applicable, because only one intermediate population was found to lack such a recombination spindle. With regard to the Benicia population, the second hypothesis seems a better one; it appears likely that the Benicia population has been undergoing recombination and "shuffling" for a longer time than have the three putative hybrid populations in the vicinity of Mount Diablo.

That hybridization is taking place between *Q. agrifolia* and *Q. wislizenii* is suggested also by the two putative hybrid trees mentioned above. In the first case, biennial acorns were found on a tree that from a morphological standpoint is predominantly *Q. agrifolia*; in the second case, annual fruit maturation occurred on a tree that is predominantly *Q. wislizenii* in morphology. It is hard to imagine a character so complex as fertilization and fruit maturation being anything but multifactorial. There is only one logical way for this character complex to enter the genotype of another species, and that is through hybridization.

Most hybrid individuals appear to be established in habitats that are nearer to populations of *Q. agrifolia*; the Junction Camp population presents such a situation. Five *Q. wislizenii* were found here in an area that has a large number of *Q. agrifolia*. To the extent that backcrossing is in evidence, it appears to be in the direction of the latter species. Also, the tree referred to previously as morphologically *Q. agrifolia*, but with the biennial fruiting characteristic of *Q. wislizenii*, was found in the same population. That it has had totally abortive acorns for at least two seasons is consistent with the hypothesis that pollination is by the abundant *Q. agrifolia* in the vicinity, and not by the relatively scarce *Q. wislizenii*, and that the pollen from a tree with annual maturation is ineffective on the stigmas of this hybrid that has biennial maturation. This hypothesis is further suggested by the fact that a large acorn crop is produced by the putative hybrid tree in the Benicia population. In the latter situation the tree is morphologically *Q. wislizenii* with annual fruit-

ing characteristic of *Q. agrifolia*; fertilization can very likely be effected by pollen of both species, since an overwintering period is not required.

Fruits are abortive on the single hybrid between *Q. kelloggii* and *Q. agrifolia* that was found. It can be inferred from this also that the pollen from a species with annual fruit maturation is unable to effect fertilization with a species having biennial maturation. The hybrid tree is surrounded by *Q. agrifolia*, which very likely pollinates most of the flowers. The pollen is then perhaps unable to live through the long overwintering period to effect fertilization the following spring. It is notable in this regard that the fruits develop as far as the overwintering stage in which the involucre enlarges, but the acorn itself does not develop.

Hybrids have been previously reported between oaks with annual fruit maturation and those with biennial maturation (Muller, 1952; Irgens-Moller, 1955). Such hybrids were obtained artificially, and involved a cross between the subgenera *Lepidobalanus* (white oaks) and *Erythrobalanus* (red and black oaks) (Irgens-Moller, 1955). The significant point for this discussion is that *Q. robur* and *Q. macranthera*, which are white oaks having annual fruit maturation, were pollinated by *Q. borealis*, a red oak having biennial fruit maturation. Reciprocal crosses, using pollen from white oaks on stigmas of red oaks, were unsuccessful. The uni-directional gene exchange proposed for *Q. agrifolia* and *Q. wislizenii* in the present study not only parallels the situation that resulted from artificial hybridization experiments between subgenera in *Quercus*, but it also suggests, contrary to published opinions (Benson, 1962), that factors other than the differences in fruit maturation may form the primary barriers to breeding between the subgenera of oaks.

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POLLEN STUDIES IN RELATION TO HYBRIDIZATION
IN *CERCIDIUM* AND *PARKINSONIA*
(LEGUMINOSAE: CAESALPINIOIDEAE)

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During a study of *Cercidium* in the Sonoran Desert (Carter, 1974a; 1974b), the hypothesis was developed that *Cercidium sonorae* is of hybrid origin and that the parental species are *C. microphyllum* and *C. praecox*. The hybrid is known to occur only within the distributional overlap of these two species.

Because interspecific hybrids commonly exhibit reduced fertility as compared to parents, and since pollen fertility may be studied by staining pollen with aniline-blue lactophenol ("cotton blue", Hauser and Morrison, 1964), pollens from samples of *C. sonorae* were tested for relative fertility. For comparative purposes, the examination of pollen was extended to include other taxa of *Cercidium* and the related genus *Parkinsonia*. Percentages of stained pollens reported in Table 1 and in the following discussion are based on samples of mostly 300 to 600 (200 to 1250) pollen grains per collection. Pollen of the *species* studied showed stainabilities of 83 to 98 percent, whereas pollen stainabilities in various *putative hybrids* varied from 5 to 76 percent (except in Kamb 2014).

In those specimens of *Cercidium sonorae* examined for presumed pollen viability, the percent of stained pollen varied from 42 to 76 percent, whereas in the putative parents, *C. praecox* and *C. microphyllum*, 89 percent or more of the pollen stained with cotton blue. One exception (Carter & Ferris 3446 with 84 percent of the pollen grains stained) is not typical *C. microphyllum* and the tree may represent a backcross between *C. sonorae* and *C. microphyllum*. The morphological characters in which *C. sonorae* resembles or is intermediate between one or the other of its putative parents are set forth elsewhere (Carter, 1974a).

Pollen stainability in a putative hybrid between *Cercidium floridum* and *C. microphyllum* (Kamb 2014 from near Sierra Pinacate, northern Sonora) is 86 percent. The specimen has leaflets larger than typical for *C. microphyllum* and more leaflets than usual in *C. floridum*; pubescence of the ovary is similar to that in *C. microphyllum*; the thorns are comparable to those in *C. floridum*. Both of the putative parents are known to occur in the area (Hastings, Turner, and Warren, 1972); in fact two sheets (DS, UC) of the Kamb collection contain branches of *C. floridum* bearing immature legumes, as well as the flowering branch of the putative hybrid; a third sheet (ARIZ) bears only a fruiting branch of *C. floridum*.

Discovery of a putative hybrid between *Cercidium praecox* and *Parkinsonia aculeata* is an interesting story. During the course of a field trip

TABLE 1. COMPARISON OF POLLEN STAINABILITIES AND SIZES IN *CERCIDIUM* AND *PARKINSONIA* AND THEIR PUTATIVE HYBRIDS. Unless otherwise noted, all collections are from Baja California Sur, Mexico, and are in the Herbarium of the University of California, Berkeley. Duplicates of the Carter, and Carter et al. collections are to be distributed.

Collection	Percent stained	Pollen size in micrometers	
		Range	Mean
<i>Cercidium floridum</i> Benth. ex Gray			
<i>Munz & Hitchcock 12166</i> : 20 mi. NE of Ogilby, Imperial Co., Calif. 6. IV. 1932.	96	24.7-29.9	27.0
<i>Carter 4359</i> : plain N of Empalme, Sonora, 6. IV. 1962.	98	24.7-28.6	26.9
<i>Cercidium macrum</i> Johnston			
<i>Palmer 125</i> : vicinity of Victoria, Tamaulipas, in 1907.	97	Not measured.	
<i>Cercidium microphyllum</i> (Torr.) Rose & Johnston			
<i>Carter & Ferris 3446</i> : Rancho Aguajito, Arroyo Gua, N of Loreto, 24.IV.1955.	84	23.4-27.3	25.1
<i>Carter 4415</i> : Rancho La Venta, 16 km W of Loreto, 21.IV.1962.	99	23.4-28.6	25.6
<i>Carter 5670</i> : 55 km E of Villa Insurgentes, 3. V.1972.	89	24.7-28.6	26.5
<i>Cercidium peninsulare</i> Rose			
<i>Carter 2595</i> : Arroyo del Salto, E of La Paz, 30.III.1949.	85	23.4-28.6	25.7
<i>Carter 4414</i> : San Javier, W of Loreto, 21.IV. 1962.	91	22.1-27.3	25.2
<i>Carter & Reese 4537</i> : San Bruno N of Loreto, 1.VI.1963.	89	23.4-27.3, 32.5-33.8	26.5
<i>Carter 5680</i> : Rancho Viejo, 39 km from Loreto on road to San Javier, 6.V.1972.	87	22.1-26.0	24.7
<i>Cercidium praecox</i> (Ruiz & Pavón) Harms			
<i>Carter & Ferris 4046</i> : Cuesta de los Encinos, SE of Cerro Giganta, 29.III.1960.	95	22.1-26.0	23.7
<i>Carter, Hastings & Turner 5576</i> : Los Hoyos, northeastern Sonora, 23.IV.1971.	96	20.8-24.7	22.8
<i>Cercidium sonorae</i> Rose & Johnston (putative parents are <i>C. microphyllum</i> and <i>C. praecox</i>).			
<i>Johnston 3877</i> : Agua Verde Bay, 26.V.1921 [iso-type of <i>C. molle</i> Johnston].	52	22.1-26.0	24.2
<i>Carter 5610</i> : Bahía Agua Verde, 23.VIII. 1971.	42	19.5-26.0	22.5
<i>Carter, Hastings & Turner 5595</i> : Guaymas to Hermosillo Highway, 0.6 mi N of Bahía San Carlos junction, Sonora, 2.V.1971.	45	22.1-27.3	24.5
<i>Carter 5679</i> : San Javier, W of Loreto, 6.V.1972.	76	18.2-24.7	22.6
<i>Cercidium texanum</i> Gray			
<i>Hedrick 258</i> : ca 8 mi. SW of Spofford, Kinney Co., Texas, 17.IV.1940.	83	Not measured.	

TABLE 1. *Continued*

<i>Parkinsonia aculeata</i> L.			
Hinton 5642: Coyuca, Guerrero, 16.II.1934 (ARIZ, MEXU).	95	23.4-29.9	27.5
Carter 4413: San Javier W of Loreto, 21.IV. 1962.	98	26.0-31.2	29.6
<i>Unnamed putative hybrid collections.</i>			
Putative parents: <i>C. floridum</i> and <i>C. microphyllum</i> :			
Kamb 2014: Molina Crater, NW of Sierra Pinacate, Sonora, 29.IV.1951 (DS, UC).	86	22.1-27.3	25.0
Putative parents: <i>C. praecox</i> and <i>Parkinsonia aculeata</i> :			
Hinton 6040 Coyuca, Guerrero, 11.V.1934. (BM, NY).	20	22.1-27.3	24.3
Hinton 9968: Coyuca, Guerrero, 25.III.1937 (ARIZ, BM, K, MEXU, NY).	21	20.8-28.6	25.4
Carter, Hastings & Turner 5575: Los Hoyos, northeastern Sonora, 23.IV.1971.	21	20.8-33.8	28.7
Putative parents: <i>Cercidium</i> sp. and <i>Parkinsonia aculeata</i> :			
Vines 142: 6 mi NW of Brownsville, Texas (US).	28	22.1-28.6, 32.5-33.8	24.8
Bone in 1972, Zapata Co., Texas (TEX).	5	20.8-28.6	24.2

in northeastern Sonora with J. R. Hastings and R. M. Turner in the spring of 1971, the senior author collected flowering material from a large tree near the small pueblo of Los Hoyos (lat. 30° 06' N, long. 109° 48' W). At the time, we considered it to be a particularly verdant tree of *Cercidium sonorae* although the collection site was more than a degree distant, in latitude and longitude; from the nearest known locality for that taxon (Hastings, Turner, and Warren, 1972). Both *Cercidium praecox* and *Parkinsonia aculeata* were growing in the vicinity and were in full flower. Subsequently, on studying the material of this collection (Carter, Hastings, & Turner 5575), it was found that the specimens exhibited certain characteristics of *Parkinsonia aculeata* (cf. Table 2). Inasmuch as both putative parents have pollen stainability of 95 percent or more, the low pollen stainability of 21 percent for this tree served to confirm the hypothesis that it was of hybrid origin. In July of the same year, Hastings returned to Los Hoyos in the hope of collecting mature legumes. He found a cleared field where the thorn-scrub vegetation had been, and only the stump of the tree remained! Extensive search in the area failed to reveal any trees comparable to the one that had been cut down. Later that year, while studying the holdings of *Cercidium* at the Instituto de Biología, Universidad Autónoma de México, the senior author noted a specimen from Coyuca, Guerrero, México,

TABLE 2. COMPARISON OF MORPHOLOGICAL CHARACTERISTICS IN SELECTED SAMPLES OF *CERCIDIUM PRAECOX*, *PARKINSONIA ACULEATA*, AND THEIR PUTATIVE HYBRIDS. Collections studied. *Cercidium praecox*: Moore, Hernández X., & Porras H. 5765, rocky plain ca 11.4 km from Tepalcatepec, on road to Apatzingán, Michoacán, 15.XI.1949 (in leaf only). Putative hybrids: a) Hinton 9968, and b) Carter, Hastings & Turner 5575 (in flower only), collection data given in Table 1. *Parkinsonia aculeata*: Hinton 5642, collection data given in Table 1. Statements and figures enclosed in brackets are based on a series of specimens in addition to those cited. The symbol \bar{x} indicates average.

CHARACTER	<i>Cercidium praecox</i>	Putative hybrids	<i>Parkinsonia aculeata</i>
Armature	one [or two] stout thorns (undeveloped branchlets) in axil of first leaf at a node	lacking	indurate petiole and rachis of first leaf developing at a node terminates in a sharp, stout spine; petiole also often bears stout, often recurved stipular spines
Petiole length (mm)	3.0–8.5; \bar{x} =6.2 [(1–) 411(–21); \bar{x} =7.6]	a) 1.5–3.5; \bar{x} =2.4 b) 1.4–6.0; \bar{x} =3.2	ca. 0.5–6.0; \bar{x} =1.4
Pinnae	not phyllodial, orbicular in cross section	not phyllodial, somewhat flattened but not winged	phyllodial, flat and narrowly or broadly winged
length (cm)	0.6–1.4; \bar{x} =1.0 [0.4–4.5; \bar{x} =1.7]	a) 4.5–7.5; \bar{x} =6.2 b) 3–11; \bar{x} =7.9	8–29; \bar{x} =19.6
width (cm)	0.3–0.8; \bar{x} =0.4	a) 0.4–0.8; \bar{x} =0.6 b) 0.4–0.6; \bar{x} =0.4	3–4; \bar{x} =3.3
Leaflets	opposite, not caducous	opposite and/or alternate, \pm caducous	opposite and/or alternate, caducous
number (on one side of pinna)	4–7 [3–17]; \bar{x} =5.8 [6.5]	a) 11–20; \bar{x} =14.1 b) 8–20; \bar{x} =15.5	19–38 [10–40]; \bar{x} =29.4
spacing	5–6/cm; \bar{x} =5.6	a) 2–3/cm; \bar{x} =2.2 b) 2/cm	1–2/cm; \bar{x} =1.5
length (mm)	3.2–4.8; \bar{x} =4 [3–8; \bar{x} =5.9]	a) 3.4–8.0; \bar{x} =6.9 b) 4–5; \bar{x} =4.4	1.6–2.0; \bar{x} =1.8
width (mm)	1.6–2.0; \bar{x} =1.7	a) 1.2–3.4; \bar{x} =2.0 b) 1.2–2.2; \bar{x} =1.6	0.4–0.6; \bar{x} =0.5
Inflorescence	[borne in usually compact clusters along mature branches and developing ahead of leaves]	a and b) open racemes on terminal and subterminal branches; developing with the leaves and equaling or exceeding the pinnae	open racemes on terminal and subterminal branches; developing with the leaves and shorter than the pinnae

TABLE 2. *Continued*

peduncle length (mm)	[0.1-6.4; \bar{x} =1.9]	a) 4-13; \bar{x} =8.6 b) 3-25; \bar{x} =14.7	10-20; \bar{x} =16
plus rachis (cm)	0.1-2.0; \bar{x} =0.9	a) 1-27; \bar{x} =18 b) 3.4-11.5; \bar{x} =7.6	4.8-17.0; \bar{x} =10.8 [6.9-23.5; \bar{x} =15.0]
Legume vestiture at anthesis	glabrous	a and b) glabrous or with a few strigose hairs	strigose
mature	flat and papery; net- veined; not or scarcely constricted between seeds; indehiscent	a) flat and papery; net-veined; not or scarcely constricted between seeds; inde- hiscent	thin-walled; enlarged over the seeds and constricted between them; longitudinally striate but veins some- what anastomosed; irregularly dehiscent
length (cm)	[3.0-5.7; \bar{x} =4.3]	a) 3.5-6.7; \bar{x} =4.5	2.5-6.0; \bar{x} =4.7 [3.0-13.5; \bar{x} =7.2]
Seeds (number)	[1-3; \bar{x} =1.4]	a) 1-2	1-4; \bar{x} =1.6 [1-6; \bar{x} =2.8]

(Hinton 9968) having vegetative characters similar to those of our Los Hoyos collection. It bore mature legumes resembling those of *C. praecox* and it had been so identified at Kew. Subsequently, in other herbaria, additional Hinton collections of this putative hybrid were noted. Their low pollen stainability of 20 percent is comparable to that of the Los Hoyos specimen. Both *Cercidium praecox* (Hinton 5455, US) and *Parkinsonia aculeata* (Hinton 5642, ARIZ) are known to occur in the vicinity of Coyuca. Comparison of these putative hybrids and their presumed parents is made in Table 2. The yellow, structurally similar caesalpinoid flowers of *Parkinsonia aculeata* and *Cercidium praecox* exhibit the same ultra-violet light absorption pattern, i.e., the median (posterior) petal is strongly absorptive and thus appears dark or "bee-purple" under ultra-violet light and the other four petals reflect ultra-violet light. In occasional specimens all five petals of *C. praecox* absorb ultra-violet light (Carter, 1974a). Field studies, such as those that Jones (pers. comm., California State University, Fullerton) has done on *C. microphyllum* and *C. floridum*, should be carried on to determine habits of the bees visiting *Parkinsonia* and *Cercidium*.

Two specimens from Texas (*Vines* 142, US, and *Bone* in 1972, TEX), which also appear to be of hybrid origin, have been referred to the senior author. Unfortunately, no field data are available as to species associ-

ated with the Bone specimen; the label on the Vines specimen states, "Growing with *Cercidium* and *Parkinsonia* in hard, dry soil; shrub 12 feet high." On the basis of morphological characters and low pollen stainability (Table 1), it is suggested that they resulted from hybridization between one of the two Texas species of *Cercidium* (*C. texanum* or *C. macrum*) and *Parkinsonia aculeata*. The Vines specimen, with a pollen stainability of 28 percent, is similar in appearance to the putative hybrids from Guerrero and Sonora (*P. aculeata* \times *Cercidium praecox*) except that the apex of the petiole is subspinescent. The Bone specimen, with only five percent stainable pollen, has shorter pinnae than the Vines specimen, opposite leaflets, and subspinescent petiole tips. Neither specimen bears any axillary thorns. The Vines specimen is in flower only, but the ovary is strigose, as it is also in *Parkinsonia aculeata* and *Cercidium texanum*. In the Bone specimen the ovary is only slightly pubescent, but the one-seeded mature legumes resemble those of *P. aculeata* in texture and venation of the valves and in being somewhat enlarged around the poorly developed seed.

Pollen of *Parkinsonia aculeata* and of the species of *Cercidium* dealt with in this study show little difference in shape under the light microscope whether unstained and acetolyzed (Erdtman, 1952, p. 6) or stained with aniline-blue lactophenol. The grains are prolate spheroidal, tricolpate, and supra-reticulate (Erdtman, 1952; Faegri and Iversen, 1964).

As seen under the scanning electron microscope, however, the general shape of the grains is different; drying and coating of the grains results in partial collapse and therefore the equatorial diameter is greatly reduced (fig. 1). Again, all except the *Parkinsonia aculeata* \times *Cercidium praecox* putative hybrids are similar to each other in appearance, but the number of granules (verrucae) within the lumina varies. This is especially noticeable in *Cercidium microphyllum* (fig. 1, c) and *Parkinsonia aculeata* (fig. 1, f); pollen from a series of specimens should be studied, however, to determine whether or not this difference between the two is constant. In pollen of other *Cercidium* taxa observed under the scanning electron microscope, the number of these granules is somewhat variable, even on a single pollen grain. Martin and Drew (1969; 1970), in their survey of southwestern pollen grains by means of the scanning electron microscope, included *Cercidium floridum*, *C. microphyllum*, and *Parkinsonia aculeata*. They state that pollen of *P. aculeata* differs from that of *Cercidium* in its relatively smaller lumina and heavier muri. There is apparently variation in these characters inasmuch as the material seen in this and a subsequent study (Carter, 1974b) does not display such differences. In *C. sonorae*, the putative hybrid between *C. microphyllum* and *C. praecox*, there are almost no aberrant-shaped pollen grains even though *C. sonorae* pollen exhibits only 42 to 76 percent staining with cotton blue. In the putative hybrid between *C. floridum* and *C. microphyllum* (Kamb 2014), also, the number of

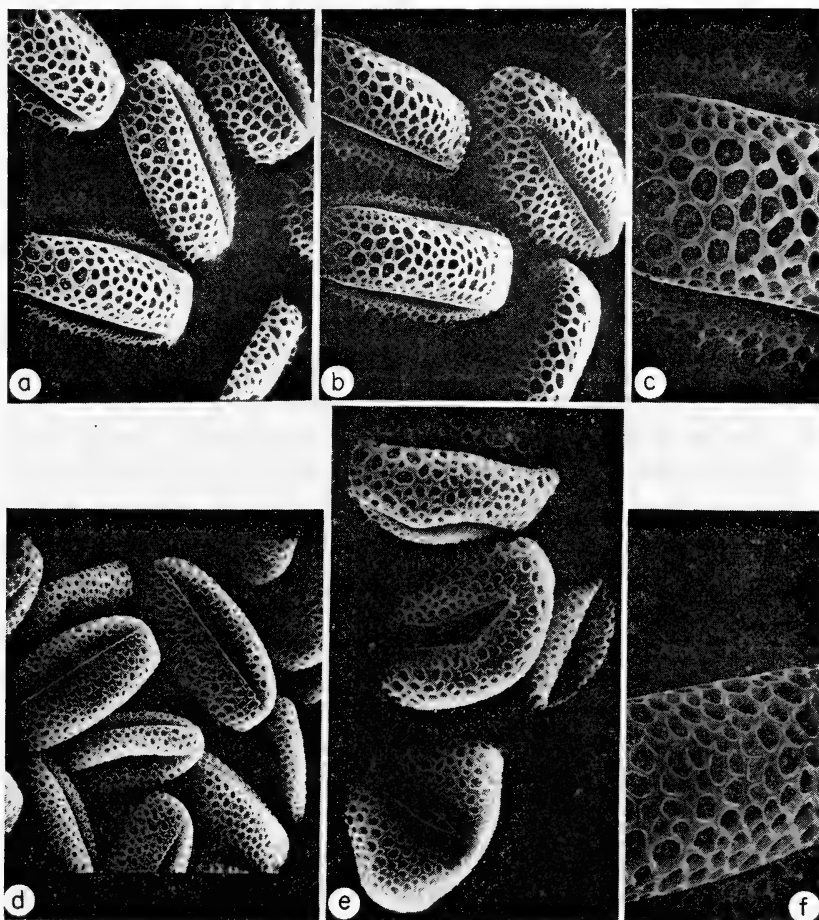


FIG. 1. Pollen of *Cercidium* and *Parkinsonia* as seen under the scanning electron microscope. *a*, *Cercidium praecox* (Carter 5576), ca $\times 1000$; *b*, *C. microphyllum* (Carter 5675, 1 km W of Las Parras summit on road from Loreto to San Javier, Baja California Sur, 6.V.1972), ca $\times 1000$; *c*, the same, $\times 2000$; *d*, *C. sonora* (Carter 5679), ca $\times 750$; *e*, putative hybrid between *C. praecox* and *Parkinsonia aculeata* (Carter, Hastings & Turner 5575), ca $\times 750$; *f*, *Parkinsonia aculeata* (Carter 5666, near km 112, NW of La Paz on highway to Villa Constitución, Baja California Sur, 3.V.1972), ca $\times 2000$. Collection data not included above are given in Table 1. The photographs were taken at the Electronics Research Laboratory, University of California, Berkeley.

aberrant grains is minimal. On the other hand, in the putative hybrids between *C. praecox* and *Parkinsonia aculeata*, with only 20 to 21 percent presumably viable pollen, there is a high percentage of malformed pollen (fig. 1, *e*) as is also the case with the two putative hybrids from Texas.

Pollen size may be affected by so many factors (Bell, 1959; Muller,

1969, p. 228) that its use as a diagnostic taxonomic character is not feasible here. In hybrids, however, variation in pollen size may be significantly greater than in species, e.g., in the *Parkinsonia-Cercidium* hybrid (Carter, Hastings, & Turner 5575) variation in pollen size is much greater than in any other taxon measured. Pollen sizes in the Sonoran Desert taxa treated, as examined under the light microscope are included in Table 1. Measurements were taken from unmistakably blue-stained grains. The range in size of pollen grains in two specimens (Carter & Reese 4537, *C. peninsulare*; Vines 142, *Parkinsonia aculeata* \times *Cercidium* sp.) is striking in that a few of the grains are unusually large (32 to 34 μ m), and there are no grains of intermediate sizes between those and the normal group measuring 28 μ m or less. In the Carter and Reese specimen only 1.7 percent of the grains measured are of the abnormally large size and in the Vines specimen, 8.2 percent. These large grains are included in calculating means.

CONCLUSIONS

That *Cercidium sonorae* has a much lower percent pollen stainability than do its putative parents, *C. microphyllum* and *C. praecox*, substantiates morphological evidence as to its hybrid origin.

The paucity of putative hybrids between species of *Cercidium* and *Parkinsonia aculeata*, the extremely low percent pollen stainabilities in such hybrids as have been noted, and the high percent of malformed pollen grains in such putative hybrids suggest that *Parkinsonia aculeata* is not as closely related to *Cercidium* as the taxa included in *Cercidium* (Johnston, 1924; Carter, 1974b) are related to each other.

ACKNOWLEDGMENTS

We are indebted to the curators of the several institutions who loaned us specimens and to the Director General de Aprovechamientos Forestales, México, for granting permission for the senior author to collect botanical specimens in Baja California and Sonora.

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NOTES AND NEWS

NEW DISTRIBUTION RECORDS OF MOSSES IN CALIFORNIA.—*Buxbaumia piperi* Best. Only two collections of the seldom seen *B. piperi* have been reported from California, one from northern Humboldt County, the other from southwestern Siskiyou County by Jamieson and Holmberg (*Bryologist* 72:72-73. 1969). In November, 1971, a small colony of *B. piperi* was discovered by Dennis Fordham and the authors on a burned redwood stump bordering a lily pond at Mendocino Woodlands Camp, 20 km east of Mendocino, Mendocino County. A year later, numerous boat-shaped sporophytes were collected from the same stump and from adjacent exposed roots in a roadcut. These collections extend the southernmost range of the species approximately 232 km. California: Mendocino Co., *Toren* 613.

Grimmia mariniana Sayre. This species, restricted to California, has been recorded only from the type locality on the summit of Mt. Tamalpais, Marin County, elevation 776 m, by Sayre (*Bryologist* 58:323-325. 1955), and from Mt. St. Helena, Napa County. In April, 1972, a third population was found at the summit of Hull Mountain in the extreme northern portion of Lake County. The colonies occurred in an open Red Fir forest at an elevation of 273 m on exposed, south-facing sandstone where snow accumulates and often persists until mid-April. This population at Hull Mountain extends the range of the species northward approximately 100 km from Mt. St. Helena and indicates that *G. mariniana* occurs in a wide range of habitats. California: Lake Co., *Toren* 779.

Grimmia occidentalis Lawt. In the spring of 1973, this semi-aquatic moss was found on serpentine rock in a creek at the State Game Refuge 2A near Lake Pillsbury, Lake County. This high elevation species was reported by Lawton at 2286-2590 m (*Moss flora of the Pacific Northwest*, Hattori Botanical Laboratory, Nichinan, Japan. 1971). However, the authors found it growing at the low elevation of 914 m, a phenomenon observed in other plant species on serpentine. Formerly reported from Wyoming, Montana, Nevada, and two localities in California, this collection extends the range of *G. occidentalis* southward from Lassen County to the Coast Ranges of Lake County. California: Lake Co., *Toren* 860, *Sigal* 63.

Grimmia heterophylla Kindb. ex Macoun & Kindb. The discovery of a well established population of this species represents a new addition to the moss flora of California. The plants were growing in loose, fragile tufts on vertical, calcareous sandstone cliffs in an exposed habitat at Hell's Peak, Lake County, at an elevation of 610 m. In association with *Grimmia heterophylla* were the other common species *G. laevigata*, *G. pulvinata*, and *G. montana*. This species has previously been recorded from British Columbia, Washington, and Idaho by Lawton (op. cit.). California: Lake Co., *Toren* 778.

The collections of the authors are in the herbarium at California State University, San Francisco. We wish to thank Dr. Daniel Norris for assistance in determining *Grimmia mariniana* and *G. heterophylla*.—DAVID TOREN and LORENE L. SIGAL, Department of Ecology and Systematic Biology, California State University, San Francisco 94132.

CHEILANTHES COOPERAE IN THE NORTH COAST RANGES OF LAKE COUNTY, CALIFORNIA.—*Cheilanthes cooperae* D. C. Eaton, endemic to California, is known from San Bernardino and Santa Barbara counties and the Sierra Nevada from Tulare County northward to El Dorado County. It has also been reported from the Mt. Shasta region, from the South Coast Ranges in San Luis Obispo County, and from the vicinity of Felton in Santa Cruz County. In January 1972, a small colony was found at Hell's Peak near Blue Lakes (T 16 N, R 10 W, S 29) at an elevation of 610 m (*Toren* 350, CAS and Calif. St. Univ., San Francisco). Subsequent exploration of the immediate area revealed that this fern was rather abundant in exposed crevices of calcareous sandstone, in association with *Penstemon corymbosus*, *Mimulus aurantiacus*, *Monardella villosa*, *Cheilanthes intertexta*, and the moss *Gymnostomum calcareum*. This population is the first record from the North Coast Ranges and extends the known range north from Santa Cruz County approximately 250 km.—DAVID TOREN, Department of Ecology and Systematic Biology, California State University, San Francisco 94132.

AUTHORSHIP OF VIOLA ORBICULATA.—In the most recent treatment of vascular plants of the Pacific Northwest (Hitchcock et al., *Vascular plants of the Pacific Northwest* 3:448, 1961.), appears the citation *Viola orbiculata* Geyer ex Hooker (London J. Bot. 6:73, 1847.). Most authors have used the same citation for this plant. The name was not validly published by Hooker according to Article 34 of *International Code of Botanical Nomenclature* (Regnum Veg. 82:40, 1972.) because he stated, "If it proves distinct, Mr. Geyer's ms. name of *V. orbiculata* should be adopted." Hooker considered the plant to be *V. rotundifolia* Michx. Wetherell (Rocky Mountain Herbarium Leaflet No. 29:7, 1958.) cited Gray (Mem. Amer. Acad. Arts n. s. 4:11, 1849.) as attributing the name to Geyer, but the name is not validly published there either, according to Article 34. Gray thought the plant was *V. sarmentosa* Dougl. The earliest valid publication of the epithet that I have found is by Gray (Syn. Fl. N. Am. 1(1):199, 1895.). Here it is published as *V. sarmentosa* Dougl. var. *orbiculata* Gray. Although Gray referred to the earlier Hooker publication, the combination must be considered as new and not a transfer because the name was not validly published by Hooker. The earliest valid publication that I have found of the epithet as a species was by Holzinger (Contr. U. S. Natl. Herb. 3:214, 1895.). This was slightly more than a month after Gray's publication but is not a transfer since Holzinger does not cite Gray and according to Article 60, "In no case does a name or an epithet have priority outside its own rank." The correct citation and the synonymy up to that time is as follows:

VIOLA ORBICULATA Geyer ex Holzinger, Contr. U. S. Natl. Herb. 3:214, 1895. —*V. orbiculata* Geyer ex Hook., London J. Bot. 6:73, 1847, pro syn. —*V. orbiculata* Geyer ex Gray, Mem. Amer. Acad. Arts n. s. 4:11, 1849, pro syn. —*V. sarmentosa* Dougl. ex Hook. var. *orbiculata* Gray, Syn. Fl. N. Am. 1(1):199, 1895.

—ROBERT D. DORN, Department of Botany, University of Wyoming, Laramie 82071.

A NEW NAME FOR A WELL-KNOWN CALIFORNIA GALIUM (RUBIACEAE).—As stated in a footnote to p. 40 of my revision, with G. L. Stebbins, of the fleshy-fruited *Galium* species of the Californias and southern Oregon (Univ. Calif. Publ. Bot. 46, 1968), it was, and still is, my opinion that the plants that have been known for 120 years as *Galium nuttallii* Gray are really two species rather than one.

Galium nuttallii Gray, as typified (San Diego, *Nuttall s.n.*, GH!), is the commoner species in San Diego Co. near the coast and in northern Baja California, occurring rarely as far north as interior Santa Barbara Co. It is represented on the Channel Islands (Santa Cruz, Santa Rosa, and Santa Catalina) by the slightly different *G. nuttallii* ssp. *insulare* Ferris. Plants of *G. nuttallii* are usually very congested, referring to the current year's growth, which forms dense masses lateral to the scaffold stems. These masses normally turn dark red at maturity. Stems are relatively smooth, and there are fewer hairs on the leaf margins. The leaves are gradually narrowed to an acute apex, with a usually persistent terminal hair, and the plant is thus rather prickly to the touch. Leaves are one-nerved, and glandular cells are generally lacking. Stomata are larger than is usually the case with diploids in the fleshy-fruited group.

The name *Galium porrigens* is proposed (the name *Galium ovalifolium* having been pre-empted) to apply to the common species that occurs from southern Oregon southward in the Coast Ranges and Sierra Nevada foothills to the San Jacinto Mountains and San Diego Co., becoming very rare in Baja California. *Galium porrigens* includes the former *G. nuttallii* ssp. *ovalifolium* (Demp.) Demp. & Steb., and *G. nuttallii* ssp. *tenue* (Demp.) Demp. & Steb. The new species differs from *G. nuttallii sensu stricto* in the abrupt, unarmed leaf apices, in the many aculeolate hairs on stems and leaf margins, and in the more lax and less red fertile branches. It differs also in the microscopic characters of smaller stomata, the presence of glandular cells on the lower leaf surfaces, and the presence of obscure supplementary leaf nerves.

The ranges of *G. nuttallii* and *G. porrigens* are distinct, but overlapping. Although there seems to be no interbreeding between the two species on the Channel Islands, there is some apparent introgression on the mainland. However, intermediate individuals and populations are few, the plants being, for the most part, readily distinguished, even where the two species occur in close proximity. There is some evidence that differential flowering dates have tended to minimize interbreeding. This matter is elaborated on p. 40 of the above-mentioned publication.

A statement of the synonymy follows:

GALIUM NUTTALLII Gray, Pl. Wright. 1:80. 1852.—Based on *G. suffruticosum* Nutt., T. & G., Fl. N. A. 2:21. 1841. Type from San Diego, *Nuttall s.n.* (GH!). Not *G. suffruticosum* H. & A., Hook. Bot. Misc. 3:373. 1833.

GALIUM NUTTALLII ssp. *INSULARE* Ferris, Contr. Dudley Herb. 4:338. 1955. Type from south of Johnson's Valley, Santa Catalina Island, *Moran 606* (DS!).

Galium porrigens Demp., nom. et stat. nov.—Based on *G. nuttallii* var. *ovalifolium* Demp., Brittonia 10:183. 1958. Type from Blue Slide, Van Duzen River, Humboldt Co., *Tracy 6816* (JEPS!).—*G. nuttallii* ssp. *ovalifolium* Demp. & Steb., Univ. Calif. Publ. Bot. 46:37. 1968.

Galium porrigens var. *tenue* (Demp.) Demp., comb. nov.—*G. nuttallii* var. *tenue* Demp., Brittonia 10:185. 1958. Type from trail to Pine Log, South Fork Stanislaus River, Tuolumne Co., *A. L. Grant 696* (JEPS!).—*G. nuttallii* ssp. *tenue* Demp. & Steb., Univ. Calif. Publ. Bot. 46:37. 1968.

Note: The use of the category subspecies within *G. nuttallii*, and the category variety within *G. porrigens* is deliberate, since in the former the separation is more clear and complete than in the latter.—LAURAMAY T. DEMPSTER, Jepson Herbarium, University of California, Berkeley 94720.

REVIEWS

The genus Lesquerella (Cruciferae) in North America. By REED C. ROLLINS and ELIZABETH A. SHAW. 288 p., 32 pl., 28 maps. Harvard University Press, Cambridge, Mass. 6 Jun 1973. \$18.00

For those of us who have been intrigued by the diminutive members of the mustard family known as *Lesquerella*, the long awaited publication of this major monograph will allow us the opportunity to finally append a few species names to collections that have been tucked away in herbarium cases for years. It is a delight to now have a key that really works, good descriptions, and some indication where the various entities grow and can be found. What is somewhat unfortunate is the unusual layout and arrangement of the book itself and the high price.

What is said by Rollins—who wrote the majority of the text—is clear and well stated. He leads the reader briefly through a characterization of the genus and then a review of the past work done on *Lesquerella*. A few paragraphs are devoted to the limits of the genus wherein Rollins discusses the well-known problems of trying to differentiate between *Lesquerella* and *Physaria*, and these from *Alyssum*. He does not accept the recent contentions of Mulligan that some species of *Physaria* should be placed in *Lesquerella*, and retains the traditional separation between the two genera on the basis that the line “between the genera is an arbitrary one, and for this reason we think it should remain as it has been accepted for many years”. Briefer sections review the breeding system, interspecific hybridization, and types of evidences available to evaluate the species. Information, usually in sufficient detail, is given on chemical criteria, chromosome numbers, and the more traditional morphological features. These data are then summarized in a section on the various taxonomic characters used in distinguishing the species and how they should be arranged into groups. Rollins and Shaw recognize ten “groups” of species, but present no formal recognition of these at any taxonomic rank.

The taxonomic section accounts for sixty-nine species—all restricted to North America except one, *Lesquerella alpina*, a polar taxon. The keys are most useful and I found only Key III difficult to use, this being due to the large number of species included within it and the complexity of the members.

The descriptions are by Shaw and are generally of sufficient detail to allow confirmation of any collection. Unfortunately, the auriculate-leaved species, which were treated in detail by Rollins in the 1950s, are only briefly treated so that one must have at hand several papers to supplement the present book for a complete understanding of these eastern United States species. The habitat and distribution data are limited to a few terse comments, but supplemented by a list of representative specimens and dot maps. What is particularly painful to me in this part of the text is the lack of full and detailed discussions about each species. Having talked with Rollins on numerous occasions about *Lesquerella*, I know he has a keen insight into these plants, but this simply is not transferred to the printed page so that much of what he knows now will go unrecorded.

The maps are clear and easy to follow (although not to find), while the plates usually leave one wishing there were more! Some of the species have photographs of the general aspect of the plant with a poor (usually fuzzy) picture of the trichomes added. However, not all species are represented, and the few excellent line drawings present only serve to tease the reader. It is too bad that the authors couldn't have found some means of having each species fully illustrated and the photographs ignored entirely.

What is most strange about this publication is the format and layout. I talked with Rollins on this matter to discover who was responsible for it—it was not Rollins or Shaw. It is so curious that one wonders where to start. The first four pages are largely (and in one case totally) blank, but then so is the top quarter of

nearly every page! It was beyond me why this was done, so I asked and was informed that it was an experiment by the press. Great! All I could think was why didn't the press let Rollins discuss the species in more detail and fill the pages up? Then the pages in my copy are cut so that the text is crooked on most pages—but I forgot to ask if this was part of the experiment too.

The strangest part of the experiment was to avoid putting the left margin flush with the column on the species descriptions and the representative specimens sections. This makes the pages look thoroughly unprofessional and sloppy. These portions of the text are distinct enough to most taxonomists, and if "eye-catchers" were needed, titles in bold-face type would have worked much better. For my part, the experiment should be written off as a total failure, and the press urged to return to the usual means of presenting taxonomic work.

And then there is the index. Or perhaps I should say, there is a section called "Index" but any resemblance with one is difficult to discover. Normally, one uses an index to find items not usually found in a table of contents—such as synonyms. Frankly, I could care less that the description of *Lesquerella alpina* is on pages 179–180, and the key to the subspecies is on page 180. What I really wanted to find was whatever happened to *L. subumbellata* Rollins? You hunt for it and you'll find it (eventually) on page 182 right under *L. alpina* var. *laevis* (Payson) C. L. Hitchc., which isn't indexed either. An index to the names would have been much more useful than the one presented.

In short, what Rollins and Shaw have done is excellent and enjoyable. What the press did with their years of hard work and research is a crime.—JAMES L. REVEAL, Department of Botany, University of Maryland, College Park 20742.

Alaska trees and shrubs. By LESLIE A. VIERICK and ELBERT L. LITTLE, JR. 265 pp., 128 figs., 128 maps, color vegetation map in pocket. U. S. D. A. Agricultural Handbook 410. 1972. \$3.25. Available from Superintendent of Documents, U. S. Government Printing Office, Washington, D. C. 20402.

This successor to *Pocket guide to Alaska trees* (Taylor and Little, 1950, USDA Handbook 5) is a much expanded and more useful work. As the title proclaims, all of the woody plants of Alaska are included, not just those species attaining the stature of trees, as in the earlier guide. The authors have divided the labor by life-forms, Little treating trees and Vierick shrubs. This has resulted in some anomalous treatments, such as Little's treatment of *Populus balsamifera* L. (Balsam Poplar) and *P. trichocarpa* Torr. and Gray (Black Cottonwood). Following extensive fieldwork in southern Alaska, Vierick reported in an earlier paper (Vierick and Foote, 1970, *Canad. Field-Naturalist* 84:169–173) that he agreed with the conclusion of Brayshaw (1965, *Canad. Field-Naturalist* 79:91–95) and Hultén (1968, *Ark. Bot.* 7:36–37), based upon the behavior of the two largely allopatric taxa in their region of sympatry in northwestern North America, that the two were conspecific, though to be recognized as subspecies. Little, who follows throughout the nomenclatural orthodoxies of his *Check list of native and naturalized trees of the United States (including Alaska)* (Little, 1953, USDA Handbook 41), takes no notice of these conclusions (despite the inclusion of two of the three cited papers in the bibliography), maintains the specific status of the two taxa, and merely remarks that the two intergrade or hybridize extensively wherever they come in contact. Aside from a very few such taxonomic quibbles, the species treatments seem quite sound. In addition to all of the data included in the "pocket guide", which are repeated here, the treatments of trees include much that is new, the remarks going far beyond the contents of the previous guide. The discussion of

Alaska vegetation and the included multicolored vegetation map are welcome additions, particularly for the layman (for whom, after all, the work is intended). The range maps, which are based upon Hultén (*Flora of Alaska and neighboring territories*, 1968), are quite clear, despite their small size. It is a pity, though, that only Alaska distribution is shown, despite the inclusion of portions of Siberia, British Columbia, and the Northwest Territories in the base map. Inclusion of the Canadian ranges, at least, would have made the volume more useful for northwest Canadian readers. The keys appear workable, those for trees being more informative than the originals in the "pocket guide". The keys to tree species in the text appear superfluous as they exactly duplicate couplets in the general key to trees, while the corresponding keys to species of shrubs are necessary and useful since the general key is just to genera. Each species treated is illustrated, the quality of representation being on the whole good. All of the illustrations of native trees (33) are reprinted from the "pocket guide" with the useful addition of winter twigs for deciduous species. The majority (22) of the tree illustrations ultimately derive from those first published in the classic *Forest trees of the Pacific slope* (Sudworth, 1908). While being very fond of that work, which is still unsurpassed for its thoroughgoing familiarity with West Coast trees, I am quite tired of seeing its illustrations repeatedly appear in books on western trees (sometimes inappropriately for Rocky Mountain forms). The present volume follows this tradition, with shrunken reproductions that have lost much of their clarity. It is time that someone should redraw the western trees to provide new insights into their characters. It would be especially pleasing to see a new figure of *Thuja plicata* Donn (Western Redcedar), for this oft-reproduced illustration is perhaps the worst, artistically and botanically, of all the figures in Sudworth's volume, and it has further decayed with reproduction. The illustrations of shrubs are as varied as their sources, and the constant change of drawing style as one turns from page to page is somewhat disturbing. Despite this juxtaposition of styles, most of the individual illustrations are at least adequate and often quite good. Whatever its drawbacks, this is a handy volume, well bound and modestly priced, that will be quite useful to any layman or botanist interested in the depauperate woody flora of the forty-ninth state.—JAMES E. ECKENWALDER, Department of Botany, University of California, Berkeley 94720.



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PLANT SUCCESSION IN THE BERKELEY HILLS, CALIFORNIA

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Secondary plant succession following the abandonment of crop agriculture has been widely studied. Little attention, however, has been given to the study of succession following the elimination of grazing livestock. Many parts of the California Coast Ranges that are adjacent to larger metropolitan areas have a history of heavy grazing followed by the elimination of livestock (Aschmann, 1959). The land use history of the Berkeley Hills of Alameda and Contra Costa counties, California, is typical of this pattern. Livestock were introduced into this area in 1776 (Halley, 1876) and their numbers increased to a peak of 185,503 animals in the decade from 1920 to 1930 (Burcham, 1957). The decline since 1930 has resulted in part from the removal of certain lands available for grazing following establishment of a watershed system and the East Bay Regional Parks. Significant vegetational changes followed elimination of grazing from the parks. The purpose of this study was to determine the pattern of succession following elimination of grazing on grassland areas in the Berkeley Hills.

STUDY AREA

The Berkeley Hills are east of San Francisco Bay adjacent to the cities of Berkeley and Oakland. They are dominated by a series of long ridges oriented along axes running from northwest to southeast. Elevations range from 90 to 580 meters.

The dominant soil type throughout the area is Los Osos adobe clay (Carpenter and Cosby, 1939). It ranges in depth from a few decimeters to about two meters and has an average depth of one meter. This soil has developed from sandstones and shales and to a lesser extent from conglomerates. Owing to the soft nature of the parent material, stony slopes, rock outcrops, and loose rocks are not abundant. The soil is subject to landslides during periods of heavy rain and as a result the surfaces of many hillsides are broken and irregular.

The area has a Mediterranean climate characterized by occurrence of frequent summer fogs and especially cool summers with no month having a mean temperature greater than 18°C (Russell, 1929). During winter, weather is dominated by a cyclone system that brings rain. Occasional intrusions of dry, cool polar air masses also occur. A climatic summary for Berkeley, the nearest station with long term records available, shows an average temperature of 9.1°C for January and 16.4°C for July based on 67 years of records. During this period, extreme maximum and mini-

mum temperatures recorded were 41.1°C and -4.1°C, respectively. Average annual precipitation is 56.8 cm with averages of 11.7 cm for January and 0.02 cm for July (U.S.D.C., 1972).

Vegetation of the Berkeley Hills as a complete physiographic unit has not been investigated. Certain portions of the area have, however, been studied (McMinn, 1916; Constance, 1932; Harris, 1927; Wright, 1928; Kraebel, 1934; Wilson and Keniston, 1942; McBride and Heady, 1968). These studies serve as a useful background in recognizing vegetation types as well as a basis for successional study. For the purpose of this report, the vegetation of the Berkeley Hills was classified into eleven types (Table 1). These were based on life form and a few dominant species. Some description, however, will be presented to complete the picture of the study area.

The grassland type occurs on a variety of exposures but is most frequently found on southwest-facing slopes. *Avena fatua*, *Bromus mollis*, and *Lolium multiflorum* are the dominant grasses in Berkeley Hills grasslands. Broad-leaved herbaceous species such as *Medicago polymorpha*, *Erodium cicutarium*, and *Geranium dissectum* are also common. All of these are exotic species that have invaded and dominated the Berkeley Hills grasslands in conjunction with the introduction of livestock from Europe (Burcham, 1957).

The baccharis brushland type varies in species composition from stands composed entirely of *Baccharis pilularis* in the shrub layer to stands in which *B. pilularis* and *Rhus diversiloba* are dominants. *Rhamnus californica* and *Rubus vitifolius* are also common in this type but seldom achieve a dominant position. The understory of baccharis brushland is characterized by an absence or very low density of herbaceous species. The type and density of herb layer species varies with the degree of crown closure and age of the baccharis brushland. Young, fairly open

TABLE 1. VEGETATION TYPES IN THE BERKELEY HILLS.

Vegetation Type	Percent	
	Area Covered	Dominant Species
Grassland	43.0	<i>Avena fatua</i> , <i>Bromus mollis</i> , <i>Lolium multiflorum</i>
Baccharis Brushland	21.0	<i>Baccharis pilularis</i> , <i>Rhus diversiloba</i>
Oak Woodland	17.2	<i>Quercus agrifolia</i>
Bay Woodland	7.4	<i>Umbellularia californica</i>
Redwood Forest	2.3	<i>Sequoia sempervirens</i>
Riparian Woodland	0.5	<i>Salix lasiolepis</i>
Knobcone Pine Woodland	0.5	<i>Pinus attenuata</i>
Manzanita-Chamise Brushland	0.4	<i>Arctostaphylos crustacea</i> , <i>Adenostema fasciculatum</i>
Coastal Sagebrush	0.1	<i>Artemisia californica</i>
Plantations:		
Eucalyptus	6.8	<i>Eucalyptus globulus</i>
Monterey Pine	0.8	<i>Pinus radiata</i>

stands exhibit an herb layer composed of grasses and broadleaf herbaceous species similar to those occurring in the Berkeley Hills grasslands. Older stands with complete crown closure are characterized by a very sparse herb layer. In many of these stands, herb density is less than one plant per ten square meters. *Rubus vitifolius*, *Scrophularia californica*, and *Satureja douglasii* are the most common species observed in the herb layer flora of the baccharis brushland type.

The oak woodland type is dominated by *Quercus agrifolia*. In most stands, *Q. agrifolia* is the only tree species. On moist sites *Acer macrophyllum* and *Umbellularia californica* may be associated with the dominant oak. *Arbutus menziesii* is found in the oak woodland type on drier sites. The shrub layer in the oak woodland is dominated by *Rhus diversiloba*, which often reaches a height of two meters or may grow as a vine up into the crowns of the trees. *Rhamnus californica*, *Rubus vitifolia*, *Symphoricarpos mollis*, *Corylus cornuta* var. *californica*, *Heteromeles arbutifolia*, *Physocarpus capitatus*, and *Rubus parviflorus* also occur as shrub layer species in the type. The herb layer of the oak woodland is rich in species in contrast to that of the baccharis brushland. The commonly occurring species are *Dryopteris arguta*, *Smilacina racemosa* var. *amplexicaulis*, *Galium aparine*, *Satureja douglasii*, and *Pteridium aquilinum* var. *pubescens*.

Umbellularia californica is the single tree dominant of the bay woodland type. A shrub layer does not normally develop beneath the *U. californica* canopy. Occasionally *Rhus diversiloba* and *Symphoricarpos mollis* may be encountered but their occurrence is rare. The herb layer of the bay woodland type can be absent or represented by a number of species tolerant to conditions of low light intensity. Among these are *Disporum hookeri*, *Trientalis latifolia*, and *Smilacina racemosa* var. *amplexicaulis*.

The other vegetation types listed in Table 1 will not be described. They represent a small but interesting proportion of the vegetation of the Berkeley Hills. They also are not part of the pattern of secondary plant succession described in this paper.

METHODS

Several methods are available for determining the pattern of plant succession. The most complete review of these methods was presented by Ludi (1930). Daubenmire (1968) discussed the more commonly used methods in his textbook on plant communities. Methods have been classified as "direct" when they are based on observation of succession on permanent plots or through the use of historical documents that give details of former vegetation. "Indirect methods" involve inference of the successional pattern. Inference is based on data or observations taken at a single time during the successional sequence. Choice of a method in any successional study depends upon availability of time, historical documents, and type of vegetation under study.

The approach used in this study was to determine the successional

position of each of the four major vegetation types in areas where grazing livestock had been eliminated. Use of "direct" methods was thought to be more positive and these methods were given priority in the study. Where sources of earlier conditions of vegetation were available, a re-survey of permanent plots or a remapping of vegetation was undertaken to identify vegetation change. When these "direct" methods could not be applied, two "indirect" methods were used. These were the stand age analysis (Clements, 1905) and maturity index (Pichi-Sermolli, 1948) methods.

Stand age analysis involves determining the age of plants in a stand and then plotting the frequency distribution of age classes for each species. Generally, climax species are characterized by J-shaped curves and sub-climax species by bell-shaped curves (Meyer and Stevenson, 1943; Braun, 1959).

Maturity index is based on the assumption that uniformity in the distribution of species in a stand increases as stands become more mature. The index is defined as the sum of the frequency percentages of all species in a stand. The index ranges from 0 to 100; the higher the index, the more mature is the stand (the closer the stand is to climax). Pichi-Sermolli (1948) has demonstrated that this relationship exists for successional sequences occurring in Europe.

RESULTS

Grassland. In studying vegetation change in grasslands removed from grazing two direct methods were used. The first was remeasurement of permanent line transects established in 1952 by Harold F. Heady (University of California, Berkeley). These line transects are 6.35 m long and extend perpendicularly across a grassland-baccharis brushland boundary. In 1965, 23 of the original 24 transects were re-examined (one could not be located) and the position of the grassland-baccharis brushland boundaries were replotted. During a 13-year period the baccharis brushland front had moved into the grassland an average of five meters. This expansion involved both the enlargement of existing plants and the addition of new plants.

The second direct method used in the grassland type involved the examination of historical documents. A map prepared by Harris (1927) delineated large areas of grassland where baccharis brushlands now dominate. Part of the area shown on the Harris Map—that part now included in Tilden Park, an area closed to grazing since the mid 1930's—was remapped in 1963. In 1927, this area, according to the Harris map, contained approximately 50 hectares of baccharis brushland. In 1963, it contained approximately 270 hectares, an increase of 220 hectares on land formerly supporting the grassland vegetation type. This change indicates a succession from the grassland type to the baccharis brushland type where livestock grazing has been eliminated.

Grasslands currently being grazed in the Berkeley Hills are relatively

free of *Baccharis pilularis* as well as other brush species. Field observations suggest that cattle browse and often pull up *B. pilularis* seedlings that they encounter in grasslands. This grazing behavior is especially evident in summer when annual grasses have dried and *B. pilularis* seedlings are among few green plants in the grassland. This impact of livestock in preventing establishment of *B. pilularis* in grassland is further evident when one compares land currently being grazed outside of the East Bay Regional Parks with those adjacent to former grasslands inside the park boundaries. The latter grasslands have been or are rapidly being invaded by *B. pilularis*.

Baccharis Brushland. Field reconnaissance of several baccharis brushlands suggested that both *Quercus agrifolia* and *Umbellularia californica* were becoming established as seedlings under the canopy of the brush species. In some brushfields it was also possible to see tree saplings extending above the canopy of the brush.

Two early vegetation maps were used to document the change indicated by the field reconnaissance. McMinn (1916) mapped Hamilton Gulch as having an area of baccharis brushland in the upper end of the gulch. His map indicates that two *Quercus agrifolia* trees were present in the upper portion of Hamilton Gulch (fig. 1). This area was remapped in 1967. Six additional trees of *Q. agrifolia* and nine of *Umbellularia californica* were found in the baccharis brushland. The remapping also illustrates an extension of the baccharis brushland into areas dominated by grassland in 1916.

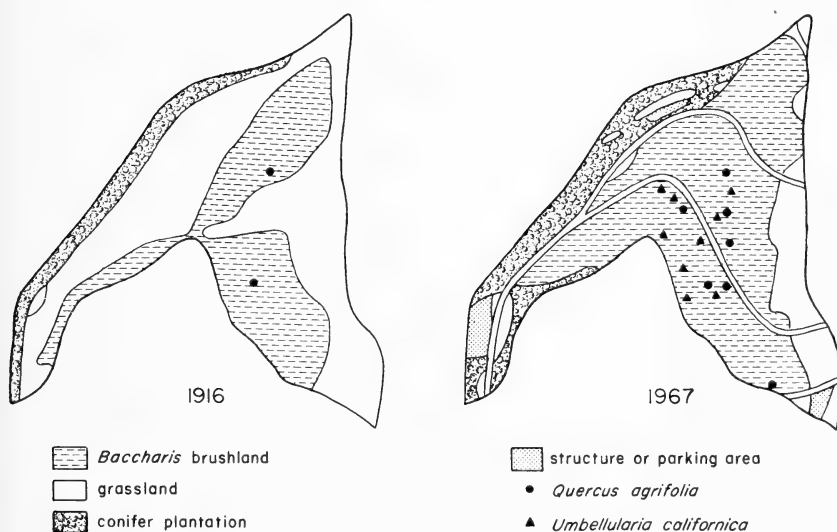


FIG. 1. Comparison of distribution of vegetation types in Upper Hamilton Gulch in 1916 and 1967.

A vegetation map of a portion of Strawberry Canyon drawn by Wright (1928) shows a large baccharis brushland in which no trees were present. This area was also remapped in 1967; nine *Quercus agrifolia* and 19 *Umbellularia californica* trees were present.

This direct use of historical documents involved baccharis brushlands that were removed from grazing in the 1920's. In areas where livestock are free to graze in baccharis brushlands, the animals seldom venture into the brushlands except along established trails. Their browsing of large plants is minimal; however, they do have an impact on seedlings along trails through the brushlands and along the margins of stands. Field reconnaissance of older baccharis brushlands accessible to livestock also indicate an invasion by *Quercus agrifolia* and *Umbellularia californica*. It would appear that the baccharis brushland type is a successional type with or without the influence of livestock. Woodland types will replace it over time. Occurrence of rather extensive older brushfields throughout the Berkeley Hills suggests that factors other than grazing have been responsible for their maintenance. All brush species common to this type are vigorous sprouters following fire (Sampson and Jespersen, 1963). Field observations of fire occurring in the Berkeley Hills over the past ten years suggest that wildfires can rejuvenate decadent baccharis brushlands. *Quercus agrifolia* and *U. californica* saplings occurring in brushfields occasionally succumb to wildfires. Those individuals that do sprout following fires are somewhat slowed down in their effort to attain tree size and form. Recurrent fire would tend to maintain a baccharis brushland. I estimate that the succession from baccharis brushland to a woodland type would be expected to take place in about 50 years in the absence of recurrent wildfires. Type of woodland (oak, bay, or mixed) depends upon those variables that affect the dispersal of tree seeds into the baccharis brushlands.

Woodland Types. No record could be found of any permanent plots having been established in the woodland types in the Berkeley Hills. Early vegetation maps of the area do not distinguish between oak woodlands and bay woodlands (McMinn, 1916; Harris, 1927; Wright, 1928; Constance, 1932; Kraebel et al., 1934; Wilson and Keniston, 1942). Therefore, indirect methods were employed to study the successional trends in the oak and bay woodlands. Specifically the stand age analysis and maturity index methods were used.

A stand age analysis was made on five oak woodland and five bay woodland stands. In each stand a 0.022 hectare circular plot was established. The age of all trees over 5 cm in diameter at breast height on each plot was determined by ring counts on increment cores taken 15 cm above the ground. All trees under 5 cm in diameter were cut off at ground level and their ages determined by ring counts on the severed sections. An age distribution curve was prepared for the oak woodlands by averaging data from the five plots (fig. 2). Likewise, a curve was prepared

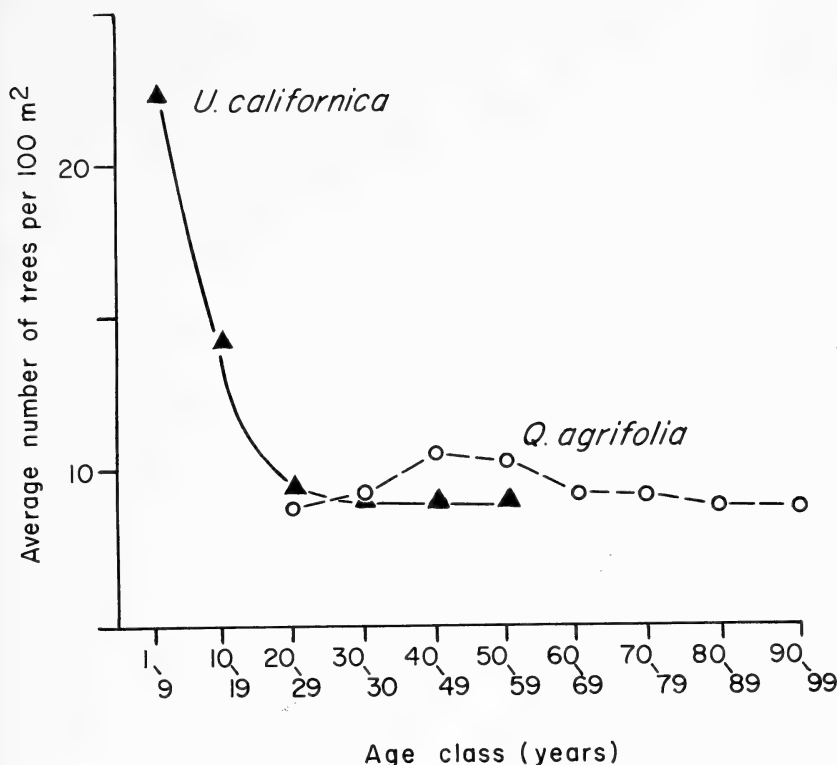


FIG. 2. Distribution of age classes of *Quercus agrifolia* and *Umbellularia californica* in five oak woodlands in the Berkeley Hills.

for the bay woodland (fig. 3). To draw the curve for each species, the average number of trees in each age class was plotted over the age class. These graphs indicate that *Quercus agrifolia* is being replaced by *Umbellularia californica* in the oak woodland type while *U. californica* is replacing itself in the bay woodland type. In both graphs *U. californica* exhibits a J-shaped curve, which is characteristic of climax species. The shape of the curve suggests that numerous seedlings are being produced. These seedlings represent a reserve from which sapling and larger sizes are being produced as openings occur in the woodland overstory. The bell-shaped curve for *Q. agrifolia* in the oak woodland stands indicates a lack of successful regeneration during the last 20 years. Curves of this shape are characteristic of sub-climax forest species that become established over a few decades then fail to produce additional seedlings. As this cohort of trees increases in age its numbers are reduced until the species eventually disappear from the site.

The second indirect method applied in investigating the successional relationship between the oak woodland and bay woodland types was the maturity index method. Five stands of oak woodland and five stands of

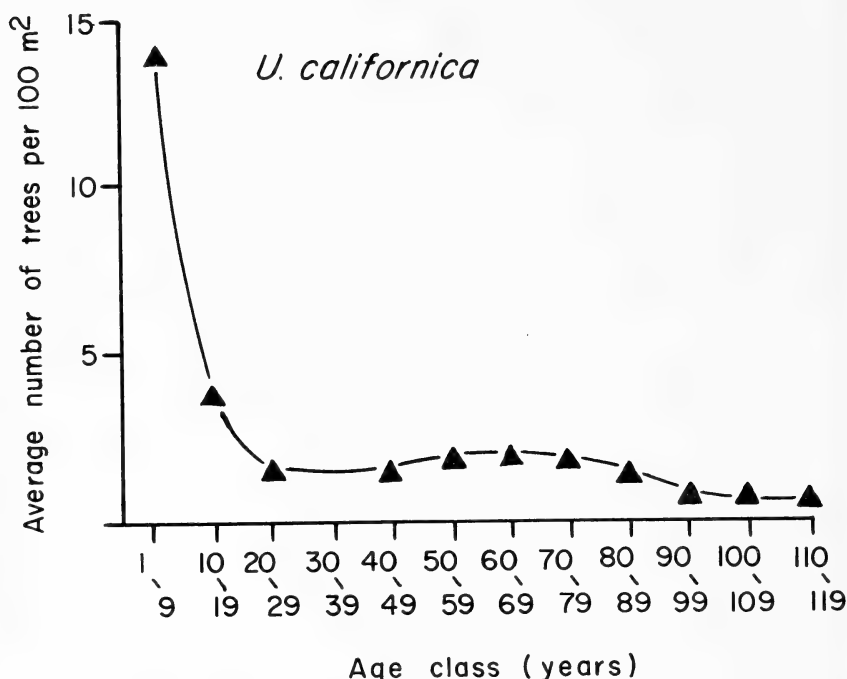


FIG. 3. Distribution of age classes of *Umbellularia californica* in five bay woodlands in the Berkeley Hills.

bay woodland occurring on northeast-facing slopes were used in determining maturity indices for each type. The frequency percentage of each species used to calculate the maturity index was based on its frequency in 100 plots (0.0929 m²) randomly located in each stand. The average maturity index for the five oak woodlands was 7.1 and the average maturity index for five bay woodlands was 11.2 (Table 2). The higher maturity index of the bay woodland indicates a greater uniformity in the distribution of species in stands of the type. This greater uniformity suggests that the bay woodland type is more "climax like" of the two types.

Use of these indirect methods to study succession in the woodland types suggests a directional movement from oak woodland to bay woodland. Furthermore, the bay woodland type exhibits characteristics associated with climax types. The impact of cattle removal on the oak and bay woodland types is difficult to assess in the Berkeley Hills due to the high density of the deer population. Both deer and cattle exhibit a preference for *Quercus agrifolia* seedlings over seedlings of *Umbellularia californica* in the Berkeley Hills. When cattle are present they hasten succession of oak woodlands to bay woodlands due to selective pressure on *Q. agrifolia* seedlings. In the areas where livestock have been removed in the Berkeley Hills, deer hunting has generally been prohibited. The

TABLE 2. SPECIES FREQUENCIES AND MATURITY INDICES. Based on 100 plots (0.02 m²) per stand in five stands of bay woodland and five stands of oak woodland.

Species	Bay Woodland Stands					Oak Woodland Stands				
	1	2	3	4	5	1	2	3	4	5
<i>Disporum hookeri</i>	67	21	26	15	18		2	2	1	1
<i>Symphoricarpos mollis</i>	43	11	5	14	7	5	20	27	9	8
<i>Trientalis latifolia</i>	40	31	21		13	16		7	9	
<i>Umbellularia californica</i>	28	43	18	34	17	1	3	3	4	2
<i>Rhus diversiloba</i>	18	16	10	17	17	30	57	14	14	31
<i>Dryopteris arguta</i>	18	10	20	10	11	21	2	10	19	7
<i>Smilacina racemosa</i> var. <i>amplexicaulis</i>	15	3	3	1		25		22	4	3
<i>Stachys rigida</i>	9	2	2	7	9		7			35
<i>Rubus vitifolius</i>	7	14	8	6	6	25	32	56	30	24
<i>Polystichum munitum</i>	4		26					1	5	2
<i>Galium aparine</i>	2			1	9	17	10	5	10	52
<i>Osmorhiza chilensis</i>	2			3	2				5	1
<i>Satureja douglasii</i>	1	6		8	2	2		13	1	8
<i>Vicia gigantea</i>	1			1				1	1	
<i>Lathyrus vestitus</i>		4		1		1	1	4	1	
<i>Fragaria californica</i>		3				1		13		
<i>Galium californicum</i>		1	4				2	3		4
<i>Rhamnus californica</i>		1				5	2	3	2	1
<i>Holodiscus discolor</i>		1					2			
<i>Aster radulinus</i>		1		4			15	17		
<i>Tellima grandiflora</i>			2							
<i>Actea rubra</i> var. <i>arguta</i>			2							1

TABLE 2, Continued.

Species	Bay Woodland Stands					Frequencies					Oak Woodland Stands				
	1	2	3	4	5	1	5	4	3	2	1	2	3	4	5
<i>Symphoricarpos rivularis</i>			1		5									1	10
<i>Ribes menziesii</i>			1												
<i>Physocarpus capitatus</i>			1												
<i>Saxifraga californica</i>				2	1										
<i>Heteromeles arbutifolia</i>				1											3
<i>Rosa gymnocarpa</i>				1											
<i>Sambucus caerulea</i>				2									1	1	
<i>Pityrogramma triangularis</i>				1											
<i>Pellaea mucronata</i>				1											
<i>Quercus agrifolia</i>										5		6	4	3	9
<i>Rubus parviflorus</i>										8			4	4	5
<i>Scrophularia californica</i>										3			2		1
<i>Lactuca virosa</i>										4			1		
<i>Chlorogalum pomeridianum</i>										5			3		
<i>Pteridium aquilinum</i> var. <i>pubescens</i>										7		2	4	2	1
<i>Prunus virginiana</i> var. <i>demissa</i>										2					
<i>Heracleum lanatum</i>										1					1
<i>Cirsium vulgare</i>										1					1
<i>Monia perfoliata</i>															7
<i>Corylus cornuta</i> var. <i>californica</i>												1	2	2	
<i>Hypochoeris glabra</i>										1					2
<i>Cornus stolonifera</i>												3			
<i>Aesculus californica</i>												2			4

<i>Sanicula bipinnatifida</i>	2	1	3	17
<i>Linaria canadensis</i> var. <i>texana</i>		1		
<i>Agrostis hallii</i>		1		7
<i>Artemisia douglasiana</i>		1	3	
<i>Marah fabaceus</i>		1		
<i>Poa pratensis</i>				2
<i>Baccharis pilularis</i>			3	
<i>Dentaria californica</i>	19	2	1	10
<i>Helenium puberulum</i>		1		
<i>Gutierrezia californica</i>		1		
<i>Stellaria media</i>		2	1	2
<i>Acer macrophyllum</i>		1		
<i>Cynoglossum grande</i>				8
<i>Ribes divaricatum</i>		1		
<i>Sonchus asper</i>				5
<i>Prunus emarginata</i>		1		
<i>Polypodium californicum</i>				1
<i>Vicia angustifolia</i>		1		
<i>Sanicula crassicaulis</i>				2
<i>Trillium ovatum</i>				1
Sum of Frequencies	255	168	150	130
Number of Species	14	16	16	20
Maturity Index	18.2	10.5	9.4	6.5
Average Maturity Index			11.6	7.1
			7.0	7.9
			31	35
			7.5	4.5
			144	260

TABLE 2. Continued.

Species	Bay Woodland Stands					Oak Woodland Stands				
	1	2	3	4	5	1	2	3	4	5
<i>Symphoricarpos rivularis</i>			1		5				1	10
<i>Ribes menziesii</i>			1							
<i>Physocarpus capitatus</i>			1							
<i>Saxifraga californica</i>				2	1					
<i>Heteromeles arbutifolia</i>				1						
<i>Rosa gymnocarpa</i>				1					3	3
<i>Sambucus caerulea</i>				2				1	1	
<i>Pityrogramma triangularis</i>				1						
<i>Pellaea mucronata</i>				1						
<i>Quercus agrifolia</i>						5	6	4	3	9
<i>Rubus parviflorus</i>						8		4	4	5
<i>Scrophularia californica</i>						3		2		1
<i>Lactuca virosa</i>						4		1		
<i>Chlorogalum pomeridianum</i>						5		3		
<i>Pteridium aquilinum</i> var. <i>pubescens</i>						7	2	4	2	1
<i>Prunus virginiana</i> var. <i>demissa</i>						2				
<i>Heracleum lanatum</i>						1				1
<i>Cirsium vulgare</i>						1				1
<i>Montia perfoliata</i>										7
<i>Corylus cornuta</i> var. <i>californica</i>						1	1	2	2	
<i>Hypochoeris glabra</i>						1				2
<i>Cornus stolonifera</i>								3		
<i>Aesculus californica</i>								2		4
<i>Sanicula bipinnatifida</i>					2		1		3	17
<i>Linaria canadensis</i> var. <i>texana</i>							1			
<i>Agrostis hallii</i>							1	3		7
<i>Artemisia douglasiana</i>							1			
<i>Marah fabaceus</i>							1			
<i>Poa pratensis</i>								3		2
<i>Baccharis pilularis</i>									1	
<i>Dentaria californica</i>					19		1			10
<i>Helenium puberulum</i>							1			
<i>Gutierrezia californica</i>								1	1	
<i>Stellaria media</i>									2	2
<i>Acer macrophyllum</i>									1	
<i>Cynoglossum grande</i>										8
<i>Ribes divaricatum</i>									1	
<i>Sonchus asper</i>										5
<i>Prunus emarginata</i>									1	
<i>Polypodium californicum</i>										1
<i>Vicia angustifolia</i>									1	
<i>Sanicula crassicaulis</i>										2
<i>Trillium ovatum</i>										1
Sum of Frequencies	255	168	150	130	185	189	174	233	144	260
Number of Species	14	16	16	20	16	24	23	31	32	35
Maturity Index	18.2	10.5	9.4	6.5	11.6	7.0	7.6	7.5	4.5	7.9
Average Maturity Index			11.2					7.1		

MADRONO

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MCBRIDE: SUCCESSION

large population of deer scattered throughout the Berkeley Hills keeps up a heavy pressure on *Q. agrifolia* seedlings. Even if cattle are removed from oak woodland stands, deer pressure alone appears high enough to prevent establishment of oaks.

Jepson (1903) described oak woodland stands in the Berkeley Hills at a time when deer had been eliminated from the Berkeley Hills. These stands also were not being grazed by livestock. In these stands all age classes were present. Jepson concluded that the oak woodland type was capable of reproducing itself because of the abundance of *Quercus agrifolia* seedlings. The absence of *Q. agrifolia* seedlings in the stands examined in the present study could reflect increased browsing pressure since the reintroduction of deer in the 1920's.

On the basis of this study, the pattern of secondary plant succession in the Berkeley Hills after removal of grazing livestock can be summarized in the following way. Grasslands are invaded by *Baccharis pilularis* and associated shrub species that replace the grassland type. *Baccharis* brushland that develops is replaced by a woodland type dominated by oak, bay, or a mixture of oak and bay. The oak woodland and oak-bay woodland are replaced finally by a bay woodland. Fire and deer play a critical role in determining the rate at which this succession progresses. The bay woodland type is capable of replacing itself under current environmental conditions.

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BOTANICAL RESOURCES OF THE HASTINGS RESERVATION, MONTEREY COUNTY, CALIFORNIA

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Hastings Reservation, Carmel Valley, California 93924

The Hastings Natural History Reservation is managed by the Museum of Vertebrate Zoology, University of California, Berkeley, and is part of the University's Natural Land and Water Reserve System. The reserve's botanical value lies not in its vegetational uniqueness but in its representative samples of south Coast Range vegetation types. The reserve furnishes good examples of foothill plant communities intermediate between coastal and Central Valley conditions. This note outlines the botanical resources of the Hastings Reservation and announces the availability of a plant list for the reserve.

HISTORICAL SETTING

Little is known of aboriginal influences on vegetation within the reserve. Small groups of Esselen Indians must have visited the region over extensive periods, for at one small campsite on the reserve they created an organic soil 125 cm deep. The Esselens probably used the area for seasonal hunting and acorn gathering. Cattle grazing from the nearest Mexican land grant, Los Tularcitos Rancho, may have affected the reserve after 1834. The initial input of Mediterranean annuals must stem from that era. Theodor Hartweg, collecting for the London Horticultural Society, probably crossed the reserve in 1846. His Carmel Valley notes include comments on lower slopes "thinly covered with oaks" and grassland "thickly covered with wild oats". American homesteaders settled

within the reserve boundaries by 1863. They cleared oaks locally for firewood and fence posts. These ranchers cultivated patches of grassland and savanna as hayfields. Sizeable portions of the reserve, however, had no gross disturbance other than grazing. In 1877 the General Land Office surveyed the area, and their map shows boundaries of some hayfields and chaparral patches. Livestock numbers and general ranching activity may have peaked around 1900.

Through the generosity of Frances S. Hastings, the Museum of Vertebrate Zoology, University of California, Berkeley, assumed control of the reserve in 1937. At that time grazing and cultivation on the former ranch ceased. The Museum's resident zoologists started intensive plant collecting. They also accumulated many plant ecological and distributional notes. A plant list based on over 3,000 specimens in the reserve herbarium was published (J. Linsdale, *Leaf. W. Bot.* 7:201-218. 1955). Visiting specialists frequently worked on systematic and cytogenetic problems of selected plants. During this period a solid base of environmental data was also gathered. Standard temperature and precipitation records are available back to 1939. Geology and soil maps were prepared. Many vegetation photographs, now over 30 years old, were taken.

In 1962 the Museum provided for a resident plant ecologist. Since then, further plant collecting has cleared up many loose ends in floristic records on the reserve. Permanent vegetation plots were established, and a variety of ecological studies were started.

PLANT COMMUNITIES

Mixed Evergreen Forest. This is the most extensive community on the reserve. It is dominated by sprouting hardwood trees, particularly oaks. At Hastings very few conifers are present in the mixture. The reserve has as good a selection of age-classes as is available in any comparable south Coast Range forest. There are three obvious local dominance phases in this low elevation forest:

Oak-madrone—open, mixed stands of *Quercus agrifolia*, *Arbutus menziesii*, *Q. kelloggii*, and other trees; well developed on the middle of long north slopes.

Coast live oak—dense stands dominated by *Quercus agrifolia*, common on lower slopes; on valley bottoms this phase becomes more open and *Q. lobata* assumes co-dominance.

Canyon live oak—dense stands dominated by *Quercus chrysolepis*, may have colonies of *Umbellularia californica*; weakly developed on north slopes and steep ravines.

Foothill Woodland. This is a well developed deciduous oak community on ridgetops and southern aspects. Stands are open with significant herbaceous cover under and between trees. *Quercus douglasii* and *Q. lobata* occur separately in pure stands and also in mixtures. These woodland or savanna stands often form transitions between Oak-madrone forest and grassland.

Riparian Woodland. Streamside communities are poorly developed on the reserve and have declined in recent decades. *Platanus racemosa* occurs along all watercourses. On open creek bottoms willows are common with clumps of *Ribes*, *Rosa*, and *Rubus*. Steep shady sections have scattered *Acer macrophyllum* and *Alnus rhombifolia* populations. The largest creek on the reserve is seldom perennial now. Portions of a smaller creek have some pools throughout the driest seasons and support some marsh species.

Chaparral. *Adenostoma fasciculatum* shrubs dominate south aspects, particularly steep mid-slope areas with shallow soils. *Ceanothus ramulosus* may be locally conspicuous, and colonies of extremely variable *Arctostaphylos glandulosa* are scattered about. Well developed communities of coastal sage scrub are absent from the reserve, but scraps of this low-shrub community border the lower margins of the chaparral. Much of the chaparral may not have burned for almost a century; small tracts burned in 1937 and 1955.

Grassland. Openings in the savanna form much of the "grassland" on the reserve. The largest naturally treeless tract is on a steep, rocky, clay soil from basalt. *Stipa pulchra* is widely distributed in the grassland, both in uncultivated areas and old-fields. This bunchgrass becomes most conspicuous in swales with deep clay soils or on some rocky ridges. Grassland species diversity is high. Many 0.1 ha plots have more than 50 species present; one plot in 1973 had 77 species present. *Bromus mollis* and *Avena fatua* are the most important annual grasses in the least disturbed parts of the grassland.

FLORISTICS

Vascular Plants. Since 1937, the approximate numbers of taxa collected on the 780 ha of the reserve are:

Families	77
Genera	296
Native species	465
Introduced species	127
Inter-"generic" hybrids	4
Inter-"specific" hybrids	8

Only 26 additional species have been found since compilation of the 1955 plant list.

Diversity within families and genera follows expected patterns. There are 50 genera of Compositae and 30 genera of Gramineae. Legumes are conspicuous in the grassland with 15 *Trifolium*, 9 *Lupinus*, and 7 *Lotus* species. The most diverse shrub genus is *Ribes* with 6 gooseberry and 2 currant species. The most important tree genus is *Quercus* with 6 species and 4 formally described hybrids.

Only one Santa Lucia Range endemic is present on the reserve, *Ribes*

sericeum. Several Santa Lucia-Gabilan Range endemics are present: *Clarkia bottae*, *Eriastrum virgatum*, *Eriogonum nortonii*, and *Mimulus bifidus* ssp. *fasciculatus*.

A few of the "native" species are probably not native locally and have reached the reserve recently. The high number of exotics (21 percent) includes 44 weeds and domestic species that disappeared from the gardens and fields a few years after farming stopped. In both uncultivated grassland and old-fields about 35 percent of the species now present introduced. It seems unlikely that many of these exotics will disappear from the grassland in the foreseeable future. One species that has either been recently introduced or else has made a dramatic recent expansion is *Draba verna*. A small population of *Bromus tectorum* discovered in 1971 has remained stable.

Non-vascular Plants. Although there have been spurts of collecting of various lower plant groups, they have received far less attention than vascular plants. Except for lichens, few specimens have been added in the last 20 years, and the names have not been checked recently. Most of the determinations for mosses were by L. F. Koch in 1951, for liverworts by A. Carter between 1941-44, and for lichens by A. W. Herre between 1941-42. Approximate numbers of taxa collected on the reserve in these groups are:

	families	genera	species
Mosses	21	46	82
Liverworts	10	10	16
Lichens	22	42	160

Interest in fungi has been rather spotty. Some 250 species have been identified, not counting the lichens. Lee Bonar collected on the reserve in the 1940's. He determined most of the specimens in the collection and described two new species from reserve material. Bonar also compiled a list of 145 fungi causing plant diseases on the reserve. Hypogaeous fungi were given special attention since they are an important rodent food. Helen Gilkey worked on the Tuberales and described two new species.

PLANT LIST AVAILABILITY

A complete plant list and bibliography may be obtained from the Hastings Reservation, Star Route Box 80, Carmel Valley, California 93924. This list contains additional environmental data, vegetation descriptions, and detailed annotations on all vascular plants.

The real resources at Hastings are not the specimens but the plants and communities available for study under relatively undisturbed conditions. Anyone wishing to use these natural area facilities for research or class purposes should contact the same address listed above.

REVIEW OF NORTH AMERICAN PACIFIC COAST BEACH VEGETATION

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The objective of this paper is to summarize, mainly through a review of the literature, beach vegetation and its phytogeography along the Pacific Coast of North America between Point Barrow, Alaska (approximately 71°N), and Cabo San Lucas, at the southern tip of Baja California (approximately 23°N , fig. 1). "Beach" is that strip of sandy land from just above mean high water to just beyond the reach of storm waves, or, if there is a foredune, to the top of the foredune. The term "strand" has often been applied to this strip of land, but it is clear from a number of floras that the concept of strand varies widely: it may apply to the very edge of shore only, or to the beach plus adjacent inland dunes, even though most dune species do not extend onto the beach. To avoid ambiguity, we have chosen the more intuitive term beach. As defined here, the beach habitat is characterized by a maritime climate, high exposure to air-borne salts and sand blast, and a shifting substrate with a low water-holding capacity and low organic matter content.

The survey of beach vegetation does not include species of adjacent habitats such as dunes, ocean-facing cliffs, salt marshes, shingle beaches, and the intertidal unless those species are also characteristic of beach vegetation. Exclusion of dune species is justified in an ecological sense, for levels of both soil- and air-borne salinity drop appreciably behind the beach (Barbour et al., 1973; Boyce, 1954; Martin and Clements, 1939; Oosting and Billings, 1942). Plants of dunes may be xerophytes, but they are not obligate halophytes (Barbour, 1970b; Martin and Clements, 1939; Purser, 1934, 1936). Kearney (1904) first raised the question of whether beach plants are halophytes, but data accumulated since then (see review by Barbour, 1970d) indicate that levels of salt spray are high, even if soil salinity levels are not. Beach plants are either facultative halophytes or salt-tolerant glycophytes.

Exclusion of cliff species, although necessary, is regrettable. On windy, rocky, open coasts, plants of ocean-facing cliffs receive considerable amounts of salt spray, enough spray to cause some authors to call them "quite salt tolerant" (Calder and Taylor, 1968) or "strongly halophytic" (Peck, 1961). However, the more stable substrate that typically consists of a developed soil with greater water holding capacity distinguishes the bluff habitat from the more xeric, sand blasted beach. Furthermore, the number of species found in this habitat is quite high, and slight changes in aspect or in access to fresh water permits normally inland species to

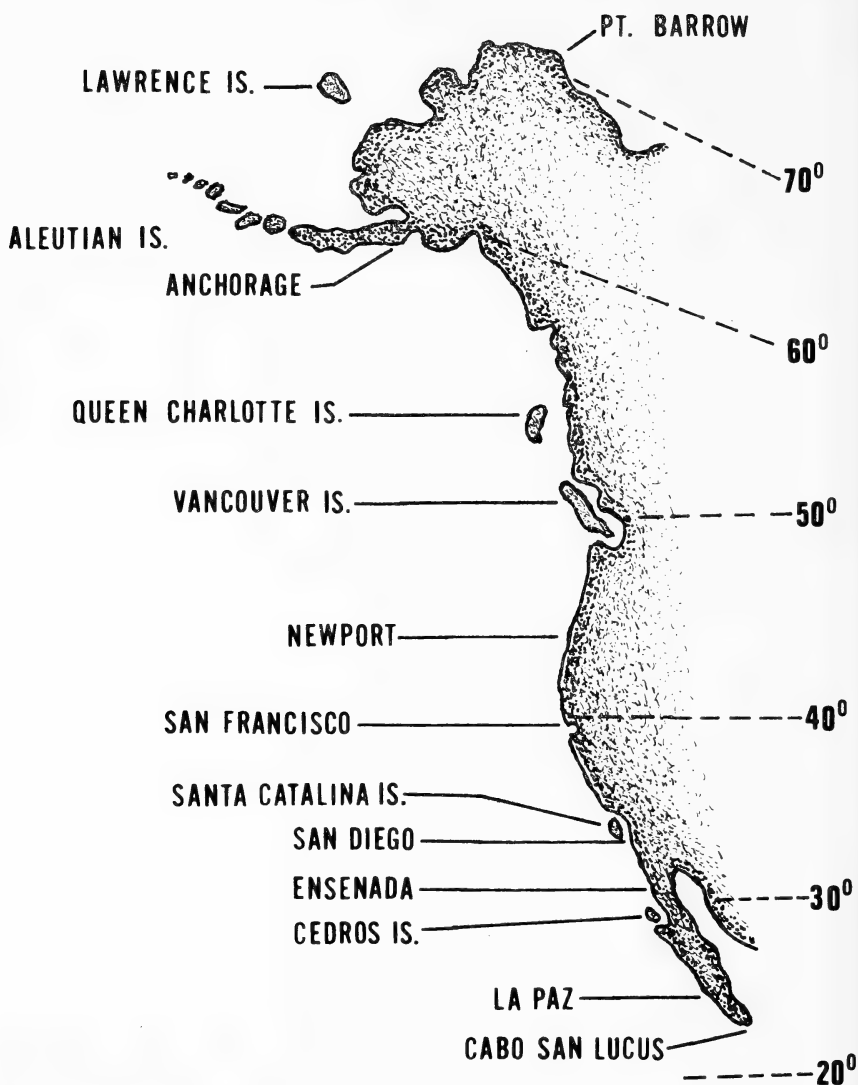


FIG. 1. The Pacific coast of North America.

occur almost side-by-side with more strictly halophytic species. Given only the information presented in the average flora, it is quite difficult to decide which species are the halophytes. At Bodega Head, California, for example, ocean-facing cliffs support truly restricted species such as *Artemisia pycnocephala*, *Eriophyllum staechadifolium*, *Armeria maritima* var. *californica*, *Jaumea carnosa*, and *Plantago maritima*, but, if a seep runs down the bank, then typically grassland species such as *Anagallis*

arvensis, *Polypogon monspeliensis*, and *Sonchus asper* follow (Barbour, 1970a).

Shingle beaches are excluded, because their substrate stability is greater than that of sandy beaches. The flora of shingle beaches is more closely related to that of salt marshes than to sandy beaches.

Throughout this paper we are concerned with those vascular plants that most characterize beach vegetation. The distribution limits that we present are for taxa where they occur on the beach. In several cases species extend further north or south than our limits, but not in the beach habitat. Furthermore, we have approximated latitudinal limits to the nearest half degree because many isolated beaches along the coast have not been botanized, especially in British Columbia and Baja California.

Much ecological work also remains to be done. Chapman (1964) states that the strand "... has not been subjected to serious study . . . and very little is known about the requirements of the individual species, or even about the nature of the environment". Few synecological and autecological studies of beach vegetation have been published. Apparently the only experimental work done on a Pacific coast beach plant is by Barbour (1970b, 1970c, and 1972b) and Barbour and Rodman (1970) on *Cakile maritima* and *C. edentula* spp. *californica*—which regrettably are not even native to the Pacific coast. They were introduced to the San Francisco area during the past 90 years and have spread rapidly north to Alaska and south to Baja California. Barbour concluded that *Cakile maritima* shows no ecotypic variation in germination, growth, or flowering along the Pacific Coast, but extrapolating from *Cakile* to other beach plants may be a tenuous procedure.

It is striking that several introduced species have spread so far and contribute so significantly to vegetation: *Mesembryanthemum edule*, two *Cakile* species, and *Ammophila arenaria*. Why are they able to do so well on the Pacific coast? Are there more unoccupied niches (if such things do really exist) on this coast than on others? Will further introductions be able to do as well or is the habitat space now filled? In this connection it may be ominous to recall a statement by Calder and Taylor (1968) that *Lolium perenne* has been introduced to beaches in the Queen Charlotte Islands for the purpose of erosion control. Already, at Sandspit, it "... is now one of the dominant grasses in this region". It appears that the South American Pacific Coast may similarly be open to invasion. Kohler (1970) points out that *Ambrosia chamissonis* and *Lupinus arboreus* have been introduced to Chile from North America, yet today they dominate beach and dune vegetation.

Cooper (1936, 1958, 1967) has recounted in detail where and when marram grass (*Ammophila arenaria*) was introduced to the Pacific Coast from Europe, and how rapidly it seems to be spreading naturally, producing in many places a foredune where none existed before. Marram

grass may “. . . in the course of decades or centuries change significantly the character of the whole dune complex”. Apparently, a foredune was not present along the central portion of the coast until *Ammophila* was introduced. We have unpublished data from Pt. Reyes, California, that further show species diversity is depressed by *Ammophila*; *Elymus*-dominated foredunes exhibit twice as many species as adjacent *Ammophila*-dominated foredunes.

The fact that few ecological studies of beach vegetation have been conducted is unfortunate, because beach vegetation may prove to be an exceptionally good “validation site” for hypotheses generated in studies of other vegetation types, where competition confounds the picture. MacArthur (1972), has hypothesized that the warm limit of any species’ range is most often determined by competition, not by climate. What happens on the strand? MacArthur (1972) and Axelrod and Bailey (1969) have independently postulated that species diversity is affected more by temperature equability than by seasonal uniformity of precipitation. We can test this along the beach, for it includes areas with both equable temperature and moisture (Washington), areas with only temperature equability (Northern California), and areas with neither temperature nor moisture equability (Southern California and Baja California). Unfortunately, considering the increasing human population and rate of destruction of beaches along some parts of the coast, beach vegetation may be a disappearing type. Judging from reviews of Oosting (1954) and Ranwell (1972), ecological studies of beach species are a bit more numerous for Japan, Great Britain, and the east coast of the United States.

SOURCE MATERIAL

Most of the information summarized in this section comes from floras. We wish to document our choice of references in some detail because they had such a strong bearing on our ultimate choice of beach species. Most of the floras lumped beach with dune or other coastal habitats, and only by elaborate cross-checking and personal observations could we determine which species listed in fact extended onto the beach. Cooper’s fine survey of Pacific Coast strand and dune flora (1936) serves as an initial, central reference. Information about Alaskan and Baja Californian floras, however, was quite limited at that time, and therefore his survey was incomplete. His approach was not ecological, but his notes on distribution do permit one to distinguish beach species from dune species.

More recent information for the north portion of the coast can be obtained from Wiggins and Thomas’ flora of the Alaskan Arctic Slope (1962), Hultén’s flora of the Aleutian Islands (1937) and his flora of Alaska (1968), which includes areas south of Vancouver Island, Young’s flora of St. Lawrence Island (1971), and Calder and Taylor’s flora of the Queen Charlotte Islands (1968). Of the four, Calder and Taylor’s

flora contains the most detailed community descriptions and habitat notes, and the Alaskan flora contains the least (but it has the best information on overall species' distributions). References to relative abundance, coupled with photographs of habitats in the texts, lead to some conclusions as to which species were most characteristic of the beach. A recent synecological paper for Amchitka Island (Amundsen and Clebsch, 1971), though short, is very helpful.

For the central portion of the coast, we utilized major reviews by Schofield (1969) and Franklin and Dyrness (1973), Jones' survey of the Olympic Peninsula (1936), Peck's Oregon flora (1961), Kumlér's study of succession on Oregon dunes (1969), Munz's California flora (1973), Barbour's extensive floristic and ecological data for Bodega Head, California (Barbour, 1970a-d, 1972a, 1972b; Barbour and Rodman, 1970; Barbour et al., 1973), Howell's Marin County flora (1970), Thomas' Santa Cruz flora (1961), Hoover's San Luis Obispo County flora (1970), an ecological survey of Morro Bay State Park by Williams (1974) and Williams and Potter (1972), Smith's brief flora of the Santa Barbara region (1952), and the autecological studies of Martin and Clements at Santa Barbara (1939). The overview of Pacific Coast vegetation by Knapp (1965) was so brief as to be only marginally useful.

For southern California and all of Baja California, we used Boughey's checklist of Orange County plants (1968), Thorne's flora of Santa Catalina Island (1967), the lay-oriented booklet on prominent plants of coastal San Diego County by Higgins (1956), and Shreve and Wiggins' classic work on the Sonoran desert (1964). Information on Baja California was especially difficult to find, and likely sources such as Nelson's major reference work on the natural resources of Baja California (1922) and the reports of many miscellaneous botanizing expeditions (e.g., Brandegee, 1889; Johnson, 1958; and Orcutt, 1885), were very disappointing in their omission of beach plants. We have relied heavily on an M.S. thesis by Ann Johnson (1973) and on personal communications from Dr. Ira Wiggins.

A number of other floras were examined, but these did not add new material beyond that found in the above references, so they will not be cited here. Some of our floristic and climatic material also appears in a review by Macdonald and Barbour (1974), but we have considerably refined their summary. In addition the following treatments were consulted for determining species' distributions outside of the area considered and for determining possible affinities of the endemic beach species: Bowden, 1957; Fernald and Weatherby, 1916; Hall and Clements, 1923; Hermann, 1960; Lewis and Oliver, 1965; Payne, 1964; Payne et al., 1973; Raven, 1969; Rodman, 1974; St. John, 1970; Small, 1895; Swallen, 1944; and Tillett, 1967.

Nomenclature in general follows Hultén (1968) for the northern portion of the coast, Munz (1968) for the central portion, and Shreve and Wiggins (1964) for the southernmost portion. The excellent five

volume flora of the Pacific Northwest by Hitchcock et al. (1969) was particularly useful because of its full treatment of nomenclatural synonyms and for its discussions of species' affinities.

CLIMATE

The Pacific Coast of North America sweeps in a broad diagonal across 48° of latitude and 55° longitude and extends from Arctic tundra to the sub-tropical southern fringe of the Sonoran Desert (fig. 1). Climatic variations are considerable, yet because the warm North Pacific Current bathes the shores of the Aleutians, southern Alaska, and British Columbia, and the cold California Current bathes the southern coastline, the change in climate is not as extreme as experienced inland over shorter distances.

Climatic parameters for selected Pacific Coast stations are shown in Table 1. We have used the unmodified Koeppen system as described by Trewartha (1954) and have not used minor changes in it suggested by Ackerman (1941). We selected only weather stations on the coast at sea level.

The maritime climate shows increasing temperature equability southward to Point Reyes, California (38°N), where it is maximum and then begins to decrease again southward. Annual precipitation, although more irregular in its pattern, shows a similar southward increase—maximizing between $59^\circ30'$ and 57°N on the Alaskan mainland and then decreasing gradually southward. Minimum annual precipitation occurs at Bahia Magdalena, Baja California ($20^\circ40'$), where it is 1/40 of that at Yakutat, Alaska. South of Bahia Magdalena annual rainfall again begins to increase. It is possible to pinpoint six major shifts of climate.

1) At about 60°N , between Anchorage and Yakutat, Alaska, climate shifts from Df (microthermal) to Cfb (mesothermal), due to warming in the winter months; in addition, precipitation increases ninefold, as one moves south from Anchorage to Yakutat.

2) At 46°N , Seaside, Oregon, Cfb shifts to Csb; that is, a Mediterranean pattern of rainfall begins here and continues south. Winter temperatures continue to rise. Summer fog is common from here south through Baja California.

3) At 37°N , between Santa Cruz and Monterey, California, Cs (mesothermal) changes to BSc (semi-arid), due to declining precipitation. Temperatures do not change markedly.

4) At about 31°N , between Ensenada and El Socorro, Baja California, BS (semi-arid) shifts to BW (arid). Again, temperatures do not markedly change, but rainfall decreases.

5) At about 29°N , between El Rosario and Punta Abreojos, Baja California, BWk shifts to BWb due to mean yearly temperatures rising above 18°C . There are not enough stations in the 3° span between El Rosario and Punta Abreojos to be very sure about the dividing line.

TABLE 1. CLIMATIC DATA FOR SELECTED STATIONS ALONG THE PACIFIC COAST. Sources: Armstrong (1971), Arias (1942), Calder and Taylor (1968), Climate of British Columbia (1944), Climatological data (1968), Eber et al. (1968), Hambidge (1941), Hastings and Humphrey (1969), Koeppen (1931), Trewartha (1954), Wiggins and Thomas (1962), and Young (1971).

No.	Station name	Latitude (N)	Annual ppt. (mm)	Number of frost-free days/year	Mean air temperature (°C)			Mean water temperature (°C)		
					Year	Coldest mo.	Warmest mo.	Coldest mo.	Warmest mo.	Koeppen category
1	Pt. Barrow, Alas.	71°20'	103	8	-12	-22	9	0	8	ET
2	Kotzebue, Alas.	66°50'	200		-6	-19	11			Df/ET
3	Nome, Alas.	64°30'	468	73	-3	-15	10			Df/ET
4	Gambell, St. Lawrence Is., Alas.	64°00'	504		-5	-17	7			ET
5	Anchorage, Alas.	61°20'	358	118	1	-12	14	4	13	Df
6	Yakutat, Alas.	59°30'	3350		3	-1	12			Cfb
7	Sitka, Alas.	57°00'	3300	157	6	0	13			Cfb
8	Sandspit, Queen Charlotte Is., Br. Co.	53°15'	1253	207	6	3	14	7	15	Cfb
9	Amchitka, Alas.	51°30'	828		4	-1	9	2	9	ET
10	Clayoquot, Victoria Is., Br. Co.	49°10'	2675	230	9	4	15	8	15	Cfb
11	Tatoosh Is., Wash.	48°25'	1950	322	9	6	13			Cfb
12	Aberdeen, Wash.	47°00'	2147	197	10	4	16			Cfb
13	Seaside, Ore.	46°00'	1085	251	11	6	16			Cf (barely)
14	Newport, Ore.	44°35'	1555	248	10	7	14	10	15	Csb
15	Eureka, Cal.	40°45'	970	328	11	8	14	11	13	Csb
16	San Francisco, Cal.	37°45'	505	356	12	10	14	11	13	Csbn
17	Santa Cruz, Cal.	37°00'	710(!)	351(!)	14	10	17			Csbn
18	Monterey, Cal.	36°40'	460	364	13	10	17			BSsbn
19	Morro Bay, Cal.	35°20'	426	320	14	11	18	13	16	BSsbn
20	Santa Catalina, Cal.	33°22'	334	365	16	12	19	14	17	BSsbn
21	San Diego, Cal.	32°40'	250	365	17	13	22			BSsbn
22	Ensenada, B. C.	31°50'	245	365	17	13	21	14	19	BSsbn
23	El Socorro, B. C.	30°20'	110	365	17	13	21			BWskn
24	El Rosario, B. C.	30°00'	83	365	17	16	22			BWskn
25	Punta Abreojos, B. C.	26°45'	103	365	21	17	28			BWshn
26	Bahia Magdalena, B. C.	24°40'	81	365	21	18	27			BWwh
27	Todos Santos, B. C.	23°25'	179	365	22	18	28			BWwh
28	Cabo San Lucas, B. C.	22°50'	250	365	24	20	29	20	28	Aw

6) At about 23°30'N, near Todos Santos, BWs (arid, summer dry) shifts to Aw (tropical, winter dry). Winter and summer temperatures rise and so does precipitation.

The possible significance of these six points to phytogeography will be discussed in a later section of this paper.

PHYTOGEOGRAPHY

Distribution Types. It should be emphasized that we are treating only characteristic beach taxa and have not attempted to assemble an exhaustive beach flora. Thus we are dealing with ecological, rather than truly floristic units.

Our review indicates that there are some 46 species that characterize beaches of the Pacific Coast of North America. These have been arranged sequentially in Table 2 by their northern range limit.

The beach taxa, at the species level, can be divided into nine distribution types (fig. 2). Table 2 lists specific and subspecific taxa, but we have found it simpler and no less precise to deal only at the species level. As circumscribed, the categories are used both to define geographic affinities of the beach flora and to distinguish possible migratory routes. I. Circumarctic: 5 species, 11 percent of the flora.

Taxa: *Festuca rubra*, *Honckenya peploides*, *Lathyrus japonicus*, *Ligusticum scoticum*, *Mertensia maritima*.

Species in this group have either circumarctic or widespread arctic distributions. The latter two species occur in both North America and Eurasia but are absent along the arctic coasts of either Siberia or Canada or both. Disruption in these otherwise circumpolar ranges can be attributed to lack of summer warmth or destructive action of pack ice (Young, 1971).

II. Beringian-Eastern North America: 5 species, 11 percent of the flora.

Taxa: *Angelica lucida*, *Conioselinum chinense*, *Elymus mollis*, *Poa eminens*, *Senecio pseudo-arnica*.

Species included here range across Beringia and extend both north and south along the Pacific Coast. Disjunct populations also occur on the Atlantic Coast of North America and in some species additional populations are found on the Great Lakes and Hudson Bay. The disjunct distributions of these species tend to support the supposition that many of the Beringian species formerly occupied greater areas in the arctic (Young, 1971).

III. Beringian: 2 species, 4 percent of the flora.

Taxa: *Carex macrocephala*, *Glehnia littoralis*.

IV. Maritime-Endemic: 13 species, 28 percent of the flora.

Taxa: *Abronia latifolia*, *A. maritima*, *Agrostis pallens*, *Ambrosia chamissonis*, *Camissonia cheiranthifolia*, *Chamaesyce leucophylla*, *Jouvia pilosa*, *Lathyrus littoralis*, *Poa douglasii*, *Polygonum paronychia*, *Suaeda californica*, *Tanacetum douglasii*, *T. camphoratum*.

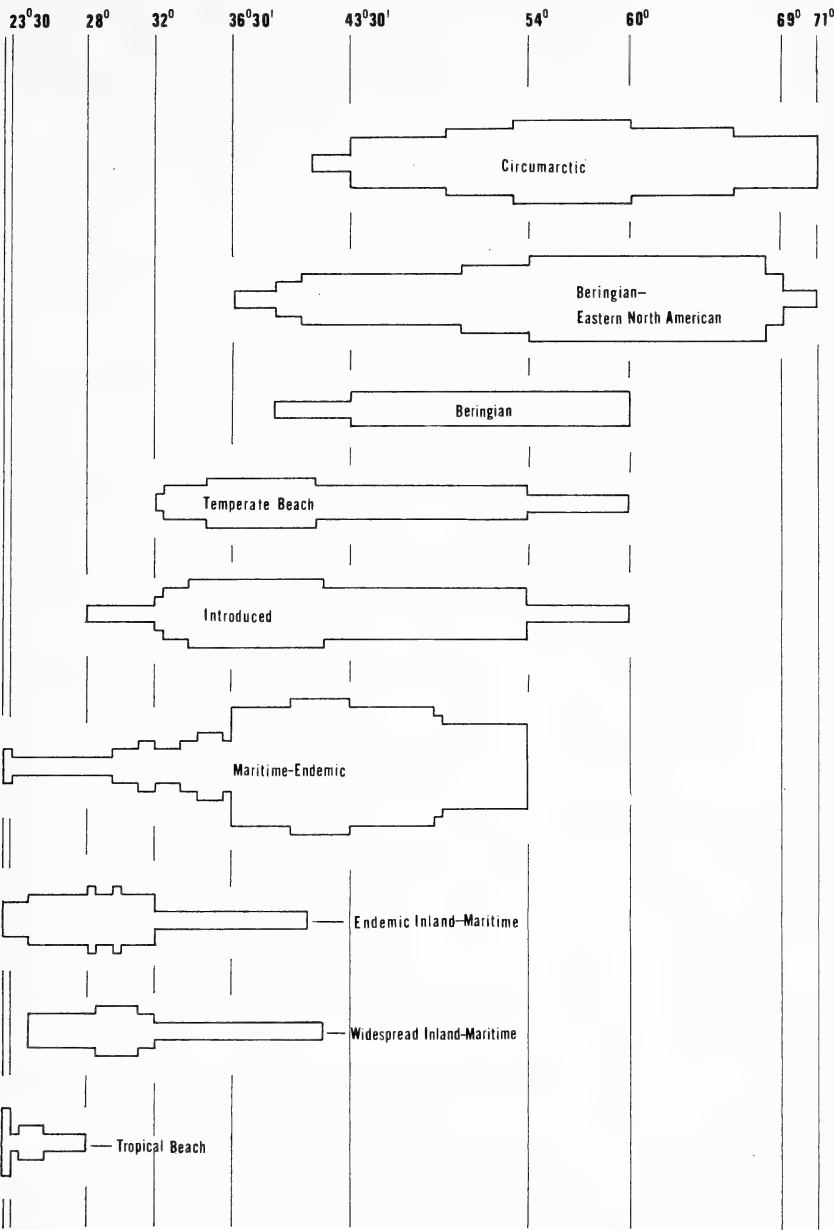


FIG. 2. Latitudinal distribution of the nine species-distribution types, from 23°30' to 71° N latitude. Width of the bars is proportional to number of species.

TABLE 2. LATITUDINAL RANGES AND DISTRIBUTION PATTERNS FOR THE CHARACTERISTIC BEACH SPECIES OF THE NORTH AMERICAN PACIFIC COAST. Latitudinal limits are to the nearest 30'. The ranges given are only for the North American Pacific Coast and only for the species as an element in the beach vegetation. Range extensions due to occurrence in non-beach habitats are given in parentheses. The numbers of the right column refer to the zone or subzone in which the taxon occurs. (1a, Arctic; 1b, Near Arctic; 2, Subarctic; 3a, Temperate North Coastal; 3b, Temperate Mediterranean; 4, Dry Mediterranean; 5, Northern Arid; 6, Southern Arid; 7, Tropical.)

Species and Distribution Pattern	Limits, N. lat.		Total Range	Zones or subzones of occurrence
	North	South		
<i>Elymus mollis</i> Trin., Beringian-E.N.A.	71°	36°30'	34°30'	1a,1b,2,3a,3b
<i>Lathyrus japonicus</i> Willd., Circumarctic				
ssp. <i>japonicus</i> , Circumarctic	71°	41°	30°	1a,1b,2,3a,3b
ssp. <i>pubescens</i> (Hartm.) C. Regel, Circumarctic	71°	52°30'	18°30'	1a,1b,2,3a
<i>Honckenya peploides</i> (L.) Ehrh., Circumarctic				
ssp. <i>peploides</i> , Circumarctic	71°	63°30'	7°30'	1a,1b
ssp. <i>major</i> (Hook.) Hult., Beringian	65°	43°30'	21°30'	1b,2,3a
<i>Mertensia maritima</i> (L.) S.F. Gray, Circumarctic	71°	53°	18°	1a,1b,2,3a
<i>Senecio pseudo-arnica</i> Less., Beringian-E.N.A.	69°	50°	19°	1b,2,3a
<i>Poa eminens</i> Presl, Beringian-E.N.A.	69°	54°	15°	1b,2
<i>Conioselinum chinense</i> (L.) BSP., Beringian-E.N.A.	68°	39°	29°	1b,2,3a,3b
<i>Angelica lucida</i> Spreng., Beringian-E.N.A.	68°	40°30'	27°30'	1b,2,3a,3b
<i>Ligusticum scoticum</i> L., Circumarctic				
ssp. <i>hultenii</i> (Fern.) Calder & Taylor, Beringian	66°	49°	17°	1b,2,3a
<i>Cakile edentula</i> (Bigel.) Hook., Temperate Strand, E.N.A.				
ssp. <i>californica</i> (Heller) Hult., Introduced	60°	32°30'	27°30'	2,3a,3b,4
<i>Fragaria chiloensis</i> (L.) Duchn., Temperate Strand				
ssp. <i>pacifica</i> Staudt., Temperate Strand	60°	35°	25°	2,3a,3b,4
<i>Glehnia littoralis</i> F. Schm., Beringian				
ssp. <i>leiocarpa</i> (Math.) Hult., Maritime Endemic	60°	39°	21°	2,3a,3b
<i>Carex macrocephala</i> Willd., Beringian	60°	43°30'	16°30'	2,3a
<i>Festuca rubra</i> L., Circumarctic				
ssp. <i>acuta</i> (Krecz. & Bobr.) Hult., Beringian	60°	43°30'	16°30'	2,3a
<i>Cakile maritima</i> Scop., Introduced	54°	28°	26°	3a,3b,4,5
<i>Ambrosia chamissonis</i> (Less.) Greene, Maritime Endemic	54°	31°	19°	3a,3b,4,5
ssp. <i>cuneifolia</i> (Nutt.) Payne, Maritime Endemic	50°	46°	4°	3a
<i>Calystegia soldanella</i> (L.) R. Brown, Temperate Strand	54°	32°	22°	3a,3b,4
<i>Ammophila arenaria</i> (L.) Link, Introduced	54°	34°	20°	3a,3b,4

TABLE 2. *Continued.*

Species and Distribution Pattern	Limits, N. lat.		Total Range	Zones or subzones of occurrence
	North	South		
<i>Abronia latifolia</i> Eschs., Maritime Endemic	54°	34°30'	19°30'	3a,3b,4
<i>Lathyrus littoralis</i> (Nutt. ex T. & G.) Endl., Maritime Endemic	54°	36°30'	17°30'	3a,3b
<i>Poa douglasii</i> Nees, Maritime Endemic	54°	36°30'	17°30'	3a,3b
ssp. <i>macrantha</i> (Vasey) Keck.	54°	39°	15°	3a,3b
ssp. <i>douglasii</i>	41°30'	36°30'	5°	3b
<i>Agrostis pallens</i> Trin., Maritime Endemic	54°	37°30'	16°30'	3a,3b
<i>Tanacetum douglasii</i> DC., Maritime Endemic	49°	40°	9°	3a,3b
<i>Polygonum paronychia</i> C. & S., Maritime Endemic	48°30'	36°30'	12°	3a,3b
<i>Camissonia cheiranthifolia</i> (Hornem. ex. Spreng.) Raim., Maritime Endemic	43°30'	33°30'	10°	3b,4
ssp. <i>cheiranthifolia</i>	43°30'	34°30'	9°	3b,4
ssp. <i>suffructicosa</i> (S. Wats.) Raven	34°30'	33°30'	1°	4
<i>Heliotropium curassavicum</i> L., Widespread Inland-Maritime				
ssp. <i>oculatum</i> (Hiller) Jtn., Widespread Inland-Maritime	42°	24°30'	17°30'	3b,4,5,6
<i>Mesembryanthemum edule</i> L., Introduced	42°	32°	10°	3b,4
<i>Mesembryanthemum chilense</i> Mol., Temperate Strand?	41°30'	32°30'	9°	3b,4
<i>Atriplex leucophylla</i> (Mcq.) D. Dietr., Inland-Maritime Endemic	41°	28°	13°	3b,4,5
<i>Tanacetum camphoratum</i> Less., Maritime Endemic	37°30'	36°30'	1°	3b
<i>Abronia maritima</i> Nutt. ex Wats., Maritime Endemic	36°	24°	12°	4,5,6
<i>Lycium brevipes</i> Benth., Inland-Maritime Endemic	32°	23°15'	10°45'	5,6,7
<i>Distichlis spicata</i> (L.) Greene, Widespread Inland-Maritime	32° (50°)	28°30' (23°15')	3°30' (26°45')	5
<i>Salicornia subterminale</i> Parish, Inland-Maritime Endemic	32°	29°30'	2°30'	5
<i>Suaeda californica</i> S. Wats., Maritime Endemic	32°	29°30'	2°30'	5,6
<i>Allenrolfea occidentalis</i> (S. Wats.) Kuntze, Widespread Inland Maritime	31°	24°30'	6°30'	5,6
<i>Frankenia palmeri</i> S. Wats., Inland-Maritime Endemic	30°	27°	3°	5,6
<i>Astragalus magdalenae</i> Greene, Inland-Maritime Endemic	28°30' (33°)	24°30' (23°15')	4°	5,6
<i>Sesuvium verrucosum</i> Raf., Tropical Strand	28°	24°	4°	6
<i>Atriplex barclayana</i> (Benth.) Dietr., Inland-Maritime Endemic	27° (32°)	23°15'	3°45'	6,7
<i>Sporobolus virginicus</i> (L.) Kunth, Tropical Strand	25°30'	23°15'	2°15'	6,7
<i>Chamaesyce leucophylla</i> (Benth.) Millsp., Maritime Endemic	24° (24°30')	23°15'	45'	7

TABLE 2. *Continued.*

Species and Distribution Pattern	Limits, N. lat.		Total Range	Zones or subzones of occurrence
	North	South		
<i>Jouvea pilosa</i> (Presl.) Scribn., Maritime Endemic	23°30'	23°15'	15'	7
<i>Ipomoea brasiliensis</i> (L.) Sweet, Tropical Strand	23°30'	23°15'	15'	7
<i>Ipomoea stolonifera</i> (Cyr.) Gmel., Tropical Strand	23°30'	23°15'	15'	7
<i>Scaevola plumeri</i> (L.) Vahl, Tropical Strand	23°30'	23°15'	15'	7

These taxa are endemic to the Pacific Coast of North America and are restricted to maritime habitats. Their apparent inability to move inland limits them to coastal or oceanic migratory routes. Both *Atriplex barclayana* and *Astragalus magdalenae* have endemic maritime subspecies, but since other elements of the species occur inland they are treated in the Endemic Inland-Maritime group.

The relationships of the endemic strand flora appear to be complex. When classified on the basis of closest probable affinities the endemic species fall into four groups: 1) species with Arctic or Beringian affinities, *Polygonum paronychia*, *Tanacetum camphoratum*, *T. douglasii*; 2) species with affinities to inland taxa of mesic temperate areas, *Agrostis pallens*; 3) species with affinities to inland taxa of arid areas, *Abronia latifolia*, *A. maritima*, *Ambrosia chamissonis*, *Camissonia cheiranthifolia*; and 4) species whose affinities are not readily apparent, *Jouvea pilosa*, *Lathyrus littoralis*, *Suaeda californica*, *Poa douglasii*, *Chamaesyce leucophylla*.

Nine of the endemic species occur in the temperate region between 54° and 36°30'N latitude, with their ranges centering around 41°. Three species have arctic affinities, three have arid-inland affinities, while only *Agrostis pallens* shows affinities with the adjacent mesic inland flora. Of the remaining four endemic maritime species, only *Abronia maritima* shows possible arid-inland relationships. The affinities of the other three species are obscure.

V. Endemic Inland-Maritime: 6 species, 13 percent of the flora.

Taxa: *Atriplex barclayana*, *A. leucophylla*, *Arthrocnemum subterminale*, *Astragalus magdalenae*, *Frankenia palmeri*, *Lycium brevipes*.

Unlike the endemic maritime taxa, these species also occur in inland habitats. They are endemic, then, to western North America. *Astragalus magdalenae* and *Lycium brevipes* are found on gravelly or sandy areas inland; the other members of the group occur in saline or alkaline situations. In contrast to the maritime endemics that are predominately in the mesic latitudes, the inland-maritime endemics are found mainly in the arid regions between 32° and 24°N (*Atriplex leucophylla* forms the only exception, extending north to 41°).

Both *Astragalus magdalenae* and *Atriplex barclayana* have subspecies restricted to either maritime or inland areas, but there is no evidence of any morphological divergence between the inland and strand populations for the other four species in the endemic inland-maritime group.

There is a total of 19 endemic species on the Pacific Coast beaches accounting for 41 percent of the beach flora, which reflects the high degree of isolation of the Pacific Coast. Whether the inland-maritime species are paleoendemics having utilized overland migratory routes to reach the Pacific coast from other oceanic shores is not evident from the fossil record. Present day distributions and taxonomic affinities strongly suggest *in situ* evolution.

VI. Widespread Inland-Maritime: 3 species, 6 percent of the flora.

Taxa: *Allenrolfea occidentalis*, *Distichlis spicata*, *Heliotropium curassavicum*.

The three species included here are similar to those in the Temperate and Tropical Strand elements in that they occur on the beaches of more than one ocean or continent. However, their ability to occupy arid, saline or alkaline inland habitats provides them with migratory routes not open to species limited to the oceanic strand. In the *Distichlis spicata-stricta* complex, inland forms can be distinguished from coastal ones. If these forms represent ecotypes then one must allow for their multiple development or else assume that the migration routes for the coastal forms are limited to the oceanic strand. The former assumption could help explain the taxonomic difficulties found in the complex.

VII. Temperate Beach: 3 species, 6.5 percent of the flora.

Taxa: *Calystegia soldanella*, *Fragaria chiloensis*, *Mesembryanthemum chilense*.

As treated here the Temperate Beach element consists of species found on the beaches of more than one ocean or continent, but whose ranges do not extend inland or into arctic or tropical latitudes. The paucity of such taxa on the North American Pacific coast demonstrates its isolation from temperate oceanic migratory routes. How did these three species arrive?

Based on its fruit morphology *Fragaria chiloensis* is certainly an endozoochore rather than a hydrochore. Van der Pijl (1969) does not consider *Fragaria* as "typically ornithochorous" because its fruits possess an odor. However, given the disjunct occurrence of ssp. *pacifica* in temperate North and South America and Hawaii, bird dispersal seems reasonable.

Calystegia soldanella and *Mesembryanthemum chilense* appear to be the only Temperate Beach species for which widespread dispersal by ocean currents can be invoked, and the status of the latter as a native is open to question (see Moran, 1950). The disjunct occurrence of the two species in both the north and south hemispheres raises the possibility that, like *Cakile*, their present ranges may be the result of early introductions in ship ballast (Barbour and Rodman, 1970).

VIII. Tropical Beach: 5 species, 11 percent of the flora.

Taxa: *Ipomoea brasiliensis*, *I. stolonifera*, *Scaevola plumeri*, *Sesuvium portulacastrum*, *Sporobolus virginicus*.

Tropical Beach species are of relative minor importance in the area of discussion since they are limited to the tip of Baja California. Their migratory routes from continent to continent are essentially oceanic, distinguishing them from the Widespread Inland-Maritime species capable of utilizing overland routes.

IX. Introduced species: 4 species, 9 percent of the flora.

Taxa: *Ammophila arenaria*, *Cakile endentula*, *C. maritima*, *Mesembryanthemum edule*.

Introduced species, with the possible exception of *M. edule*, have become dominant elements in the beach vegetation over much of the temperate region. Given their importance in the vegetation and the fact that we are dealing here with ecological and not floristic units, we have included them in our analysis of the beach flora. For the same reasons Kohler (1970) found it necessary to utilize exotics in his classification of the Chilean strand vegetation.

As a group, the introduced species range from 60°N to 28°N, with the center of their distribution at 41° in the temperate region (54–36°N). The apparent lack of exotic taxa in the arctic and tropical regions considered in this paper could be due to the continuous nature of their respective migration routes, species capable of utilizing them have already attained their potential distributions.

The success of introduced taxa on the temperate Pacific coasts of both North and South America may be analogous to island situations, where incidence of new arrivals is too low to provide a closed community. As a result, competitive interaction is thought to be minimal. Consequently, introductions have proven highly successful—either by filling previously unfilled niches or by aggressively replacing indigenous species (Carlquist, 1965).

Construction of Eco-floristic Zones. The beach habitat along the Pacific Coast of North America is a classic example of a latitudinal gradient. Elevation is uniform, variety of aspect and substrate are limited, and the flora is relatively impoverished. Yet, an attempt to divide the coast into homogeneous zones along this gradient is difficult since the species tend to have overlapping ranges and rarely share both northern and southern limits. Further, there are no universally accepted criteria on which to base floristic regions. For example, floristic regions as defined by Stebbins and Major (1965) are based on degree of endemism, which is generally considered an indicator of isolation, age, and/or uniqueness of habitat. At the other extreme, Young (1971) ignored endemism entirely in dealing with the arctic flora and based his zones on coincidence of the northern limits of taxa.

In defining our eco-floristic zones, we have emphasized regions where abrupt and marked floristic changes occur. To locate such regions, the beach flora for each 30' of latitude was determined using the ranges given in Table 2. The assumption is made that a species' range is continuous between the extremes. The floras between adjacent 30' segments were then compared for similarity using Sorensen's coefficient of community (K; Sorensen, 1948).

$$K = \frac{2 \times \text{species in common, 30' segments A and B}}{\text{species in A} + \text{species in B}}$$

The resulting K values are shown in Table 3. The 30' segments generally show a high degree of similarity to adjacent segments; however, some segments do show an abrupt loss in similarity when compared to their adjacent segment(s).

The 30' segment having the lowest K value was selected as a provisional boundary segment (PBS) and each successive adjacent 30' segment to the south of the PBS was tested by similarity against it. Typically, K decreased gradually at a relatively uniform rate with increasing distance from the PBS. Once K dropped below 0.50 further testing of more distant segments was discontinued. The PBS and the adjacent series of continuous 30' segments to the south having $K > 0.50$ were considered a protozone.

TABLE 3. FREQUENCY OF OCCURRENCE OF K VALUES. An asterisk indicates less than five species in that segment's flora. The northern boundaries of the 30' segments are listed.

K	Number of occurrences	30' segment of occurrence
1.00	61	All segments not shown below.
0.98	3	53°, 40°30', 41°30'
0.97	3	50°, 48°30', 40°
0.96	3	36°, 35°, 34°30'
0.95	6	49°, 42°, 41°, 34°, 34°30', 30°
0.94	3	66°, 39°, 37°30'
0.93	1	25°30'
0.89	3	43°30', 31°, 29°30'
0.87	2	32°30', 28°30'
0.86	2	68°, 27°
0.83	1	36°30'
0.80	2	69°*, 28°
0.79	1	60°
0.77	1	24°30'
0.74	1	54°
0.67	2	24°*, 23°30'
0.62	1	32°

There is some empirical evidence that the 0.5 level of similarity marks the lower limit of homogeneity within important vegetational units. Both Sorensen (1948) in Denmark and Looman and Campbell (1960) in Saskatchewan found that stands within the same Braun-Blanquet association or subassociation shared K values of 0.5 or above. However, our values will not be strictly comparable, because those investigators compared complete species lists of plants, not just characteristic species, as we have done.

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The northern 30' segment adjacent to the original PBS was then utilized as a new PBS and successive adjacent northern segments tested against it for similarity until a northern protozone could be delimited.

A 30' segment showing the next lowest K value was then selected from the original list (Table 3) and the entire process repeated, forming two more protozones. Selection of new PBS's on the basis of their K value and subsequent protozone formation was continued until each 30' segment of the coast was included in at least one protozone. (Those 30' segments having four or fewer species in their flora were temporarily rejected as PBS choices. We found K to be unreliable when either A or B had less than five species.)

All 30' segments could be assigned to a protozone after utilizing the five lowest PBS's, i.e., 32°, 23°30', 54°, 24°30', and 60°N. However, several of these protozone boundaries were in latitudes of a very low rate of species change. The boundary at 41°N, for example (fig. 3), showed 30' segments just north and south to have K values of 0.95. Operationally, our method was to continue to select more PBS's until the protozone boundaries had a K value (adjacent 30' segments) lower than that for remaining PBS's in Table 3. It was necessary to select two more PBS's (28°, 36°30') and form four additional protozones before maximum cleavage between all protozones was achieved (fig. 3). From this, we made our final selection of appropriate boundaries and zones.

The following criteria were utilized in selecting these final boundaries: 1) the zones had to be discrete and not overlap; 2) all 30' segments had to be assigned to a zone; 3) abrupt changes in similarity were favored over gradual changes; and 4) a 30' segment had to have a K value of 0.50 or greater with both boundaries of its zone. The resulting classification is shown in Figure 4 and tables 4 and 5.

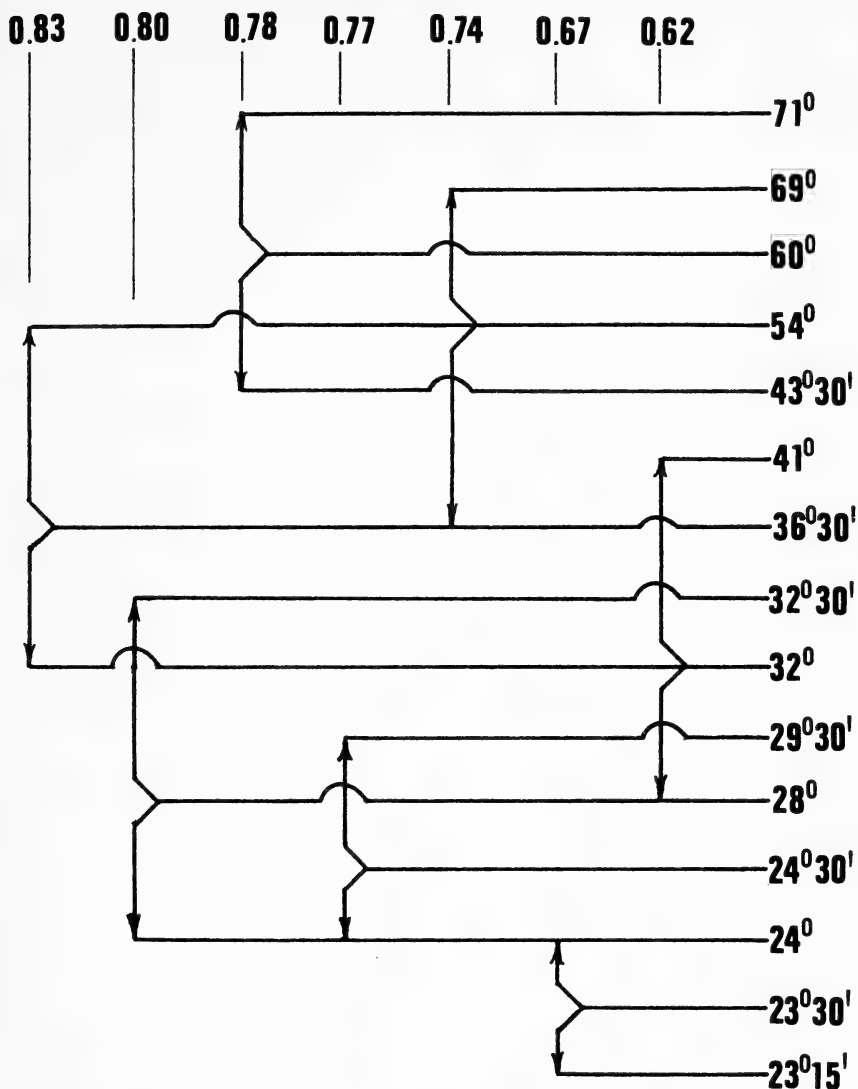


FIG. 3. Diagrammatic representation of the protozones and PBS's, from which the final, non-overlapping zones were drawn (Fig. 4). Figures on the extreme right are K values for the 30' segments just above and below the latitudes shown. The figures along the bottom indicate the K values of the seven PBS's used (e.g., 0.62 refers to the PBS at 32°N).

Discussion of the Zones. Species comprising beach vegetation in the Arctic zone are widespread strand plants with Circumarctic or Beringian-Eastern North America distributions. All of the species also occur in the Subarctic zone and most extend southward to the Temperate zone as well.

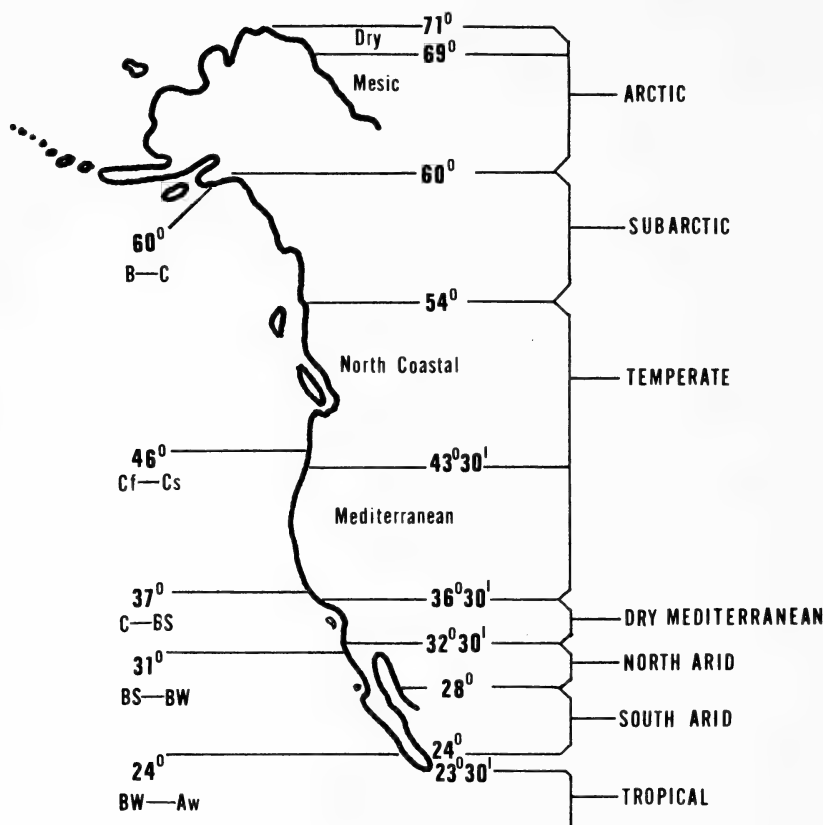


FIG. 4. Pacific coast eco-floristic zones and subzones and major climatic boundaries (Koeppen system).

The southward increase in the Arctic beach flora is a phenomenon of the arctic flora in general and can be correlated with increasing warmth, rainfall, or equability (Merriam, 1894; Nordenskjöld and Meckling, 1928; Kimble and Good, 1955; Hopkins, 1959; Young, 1971). Young divided the arctic flora into four zones that he correlated with available summer warmth. The sub-boundary at 69°N between the Dry Arctic and the Mesic Arctic beach flora does appear to correspond to the boundary between Young's zones 2 and 3. Other than this one exception, the distributions of the Arctic and Subarctic beach taxa fail to coincide with Young's zonation. Young attributed this discrepancy in distribution between the beach species and the rest of the Arctic flora to the destructive action of pack ice and depression in summer warmth found in a strongly maritime environment.

The Subarctic zone is composed primarily of Arctic, Beringian-Eastern North American, and Beringian taxa that in a group continue to influence the beach flora south to 43°30'N—the southern limit of the

TABLE 4. COEFFICIENT OF SIMILARITY BETWEEN THE ECO-FLORISTIC ZONES AND SUBZONES. The number of species shared between two zones is given on the top line of a row and the K value for the two zones is given on the second line (e.g., zones 4 and 5 share 5 spp. and have a K value of 0.40).

	1a	1b	2	3a	3b	4	5	6	7
1a, Dry Arctic	4								
	1.00								
1b, Mesic Arctic	4	9							
	0.62	1.00							
2, Subarctic	4	9	14						
	0.44	0.79	1.00						
3a, North Coastal Temperate	4	9	12	23					
	0.30	0.56	0.70	1.00					
3b, Mediterranean Temperate	2	4	7	17	23				
	0.15	0.25	0.38	0.74	1.00				
4, Dry Mediterranean	0	0	2	7	12	13			
	—	—	0.15	0.39	0.67	1.00			
5, North Arid	0	0	0	2	4	5	12		
	—	—	—	0.11	0.23	0.40	1.00		
6, South Arid	0	0	0	0	1	2	6	9	
	—	—	—	—	0.06	0.18	0.57	1.00	
7, Tropical	0	0	0	0	0	0	1	3	8
	—	—	—	—	—	—	0.10	0.35	1.00

North Coastal Temperate subzone. While the floristic importance of this group is minimal below $43^{\circ}30'N$, *Elymus mollis* still continues to be an important dominant south to $36^{\circ}30'N$ (Cooper, 1936).

Increase of the beach flora on the southern edge of the Alaskan peninsula coincides closely with the northern limits of Van Dyke's (1919, 1929) Vancouverian faunal area and with the boundary between Koepen's microthermal (D) and mesothermal (C) climate types. The criterion for separating the two climates is whether the mean temperature of the coldest month is above or below $-3^{\circ}C$, which supposedly shows a rough correlation with the southern limits of frozen ground and snow cover lasting for a month or more (Trewartha, 1954). If one uses Ackerman's criterion of $0^{\circ}C$ rather than $-3^{\circ}C$ for separating the C and D climates, then the southern limit of the D climate corresponds to the boundary between the Subarctic and Temperate beach zones at $54^{\circ}N$ latitude. At any event, the close coincidence of the floristic boundaries with a change in severity of winter cold, appears to contradict the tenet that summer warmth alone is the major climatic factor controlling the northern limits of plant distribution in arctic-alpine areas (see, for example, Daubenmire, 1954).

The Temperate zone, covering $17^{\circ}30'$ of latitude, is the largest of the floristic zones. It is characterized by a large endemic element and a high rate of species turnover between Arctic-Beringian species and endemic taxa (see fig. 2 and Table 5). Minor shifts occur in the flora between

TABLE 5. FREQUENCY OF OCCURRENCE OF DISTRIBUTION-TYPES IN THE ECO-FLORISTIC ZONES. Top line of each row gives the number of species of the distribution-type occurring in the zone and its percentage of the zone's flora. The second line of each row gives the percentage of the total number of species in the distribution-type which occur in the zone.

Zone or subzone (and total no. spp.)	Distribution types (and total number of species)								
	Circumarctic (5)	Beringian-E.N.A. (5)	Beringian (2)	Temperate Beach (3)	Introduced (4)	Maritime-Endemic (13)	Endemic Inland-Maritime (6)	Widespread Inland- Maritime (3)	Tropical Beach (5)
1a, Dry Arctic (4)	3;75	1;25							
	60	20							
1b, Mesic Arctic (9)	4;44	5;56							
	80	100							
2, Subarctic (14)	5;36	5;36	2;14	1;7	1;7				
	100	100	100	33	25				
3a, North Coastal Temperate (23)	5;22	4;17	2;9	2;9	3;13	7;30			
	100	80	100	67	75	56			
3b, Mediterranean Temperate (23)	1;4	3;13	1;4	3;13	4;17	9;39	1;4	1;4	
	20	60	50	100	100	69	17	33	
				3;23	4;31	4;31	1;8	1;8	
4, Dry Mediterranean (13)				100	100	31	17	33	
					1;8	3;25	5;42	3;25	
				25		33	83	100	
5, North Arid (9)						1;11	4;44	2;22	2;22
						11	67	67	40
6, South Arid (9)						2;25	2;25	0	4;50
						22	33	0	80
7, Tropical (8)									

50° and 48°30'N where two endemic species (*Tanacetum douglasii*, *Polygonum paronychia*) reach their northern limits and two Arctic species (*Senecio pseudo-arnica*, *Ligusticum scoticum*) reach a southern limit. Replacement of Arctic-Subarctic elements by endemic species culminates at 43°30'N—the boundary between the North Coastal Temperate and Mediterranean Temperate subzones. While the boundary is not an abrupt one ($K = 0.89$ for 44°/43°30', Table 3), it does mark the northern and southern limits of significant influence by the Dry Mediterranean and Subarctic floras respectively. The Temperate Mediterranean subzone is characterized by a high incidence of maritime endemics (41 percent of the subzone's flora falls into this class, and 69 percent of all endemics occur in this subzone).

There is a gradual decline in summer precipitation southward in the Temperate zone with a major shift around 46°N where the climate changes from a Cf type, lacking a dry season, to a Cs type, having a summer drought. Accompanying the decline in uniformity of precipitation is an increase in temperature equability. The change in the climate type appears to have little effect floristically until 43°30'N.

The boundary between the two Temperate subzones at 43°30'N, near Coos Bay, Oregon, closely corresponds to Howell's (1957) northern boundary for the California floristic province. Inland, the Province's northern limits fall several degrees further south, along the Rogue River drainage. Stebbins and Major (1965) placed the coastal limit of the California floristic province at the mouth of the Rogue River in Oregon, approximately one degree south of Howell's line. Howell attributed the coastal extension of the California flora to "... the effect of higher summer temperatures modified by coastal fogs ... [and to] ... certain ancient rocks of the Klamath Mountain area". He did not consider the possible roles of precipitation nor the modifying effect of the maritime climate on frost. It is difficult to ascertain the role of frost on the beach flora from available data. Barbour (1970c) found that the occurrence of frost was significantly less on the beach than in adjacent dunes. It is possible that species having a low frost tolerance could extend further northward in the beach habitat than in other maritime habitats.

Because of the open nature of the vegetation it can be argued that the high rate of species turnover is due solely to differences in tolerance to the abiotic environment. However, the beach may not be as open as it appears.

The beach is a permanently disturbed habitat, the flora of which consists of pioneer or colonizing species. Yet when the California beach flora is compared to the adjacent inland pioneer (weed) flora (as compiled by Robbins et al., 1970), there is a marked difference in the proportion of annual to perennial plants. Annuals comprise 54 percent of the weed flora, but they comprise only nine percent of the beach flora. The low percentage of annuals in the beach environment could be due to difficulties experienced in seedling establishment. Barbour's (1970c,

1972b) studies on the autecology of *Cakile maritima* and *C. edentula* indicate that difficulty in seedling establishment may be due to a limited number of suitable microsites on the beach. These species are short-lived, nearly annual plants whose dimorphic fruits allow for both amphicarpy and hydrochory, which results in both extremely limited and widespread dispersal of diaspores. Barbour found nearly all *Cakile* seedlings to be located within a two meter radius of parent clumps. Thus, in behavior, *Cakile* is essentially a perennial in that once established it can maintain itself for a long period in a site. Further, he was able to attribute the replacement of *C. edentula* by *C. maritima* to the greater seed production of the latter, which increased its chances of attaining a suitable site.

Despite the high turnover rate in species, the number of species is fairly constant throughout the Temperate zone (Table 5). This uniformity in species number strongly suggests that there are a limited number of possible niches available on the beach and that we have species replacement within those finite niches in the Temperate zone. If this is true, then both the number of niches and micro-sites are limited and the chances of a seed attaining a favorable site for germination and growth is slight. As a result there is a strong selection for plants capable of retaining a site either by perennial growth or amphicarpy and competition for a site is to be expected. Thus biotic interactions must be considered in "explaining" the distribution of beach species.

Between 37° and $36^{\circ}30'N$, a decrease in precipitation marks the change from a Mediterranean (Csb) to a semi-arid (BSskn) climate. Coincident with this change in climate, there used to be a change in the physiognomy of the vegetation and in beach topography. Prior to the introduction of *Ammophila*, *Elymus mollis* was a common dominant of the beaches north of $36^{\circ}30'$ and formed a grassy foredune there, whereas both the grass and the foredune were lacking in the Dry Mediterranean zone below $36^{\circ}30'$ (Cooper, 1936). Now, *Ammophila* has spread north and south of this line and has created its own unique foredune.

A marked reduction in the beach flora also coincides with the decreased rainfall between 37° and $36^{\circ}30'N$ where five species reach their southern limits. Replacement is minimal: *Abronia maritima* is the only species to obtain its northern limits between 36° and 32° .

The sudden decline in the flora at $36^{\circ}30'N$ could also be attributed to a lack of suitable habitats. The coast from $36^{\circ}30'N$ south to $35^{\circ}30'N$ consists primarily of cliffs and bluffs with the few beaches present being shallow and short. Payne et al. (1973) argue that the Monterey Peninsula with its "harsh aspect" has served as a barrier for *Ambrosia chamissonis*; the peninsula separates the populations south of Monterey from those to the north. *Cakile* species, whose diaspores can tolerate extended immersion in salt water (Barbour, 1972b), have migrated south of the Monterey Peninsula since their introduction into the San Francisco area (Barbour and Rodman, 1970), but to what extent *Ambrosia* fruits can

tolerate salt water or utilize ocean currents for dispersal is unknown. Occurrence of *Ambrosia* on isolated cove beaches in Northern California suggests that it is not dependent on a continuous beach or dune system for dispersal (personal observations).

The boundary at $36^{\circ}30'N$ between Temperate Mediterranean and Dry Mediterranean zones corresponds closely to the faunal and floristic boundaries set by other workers. Van Dyke (1919, 1929) put the boundary between Vancouverian and Californian faunal areas near Pfeiffer Point, ca $36^{\circ}15'N$. Munz (1968) used Van Dyke's boundaries for his floristically oriented biotic provinces. Stebbins and Major (1965) considered $35^{\circ}N$ to be an important floristic boundary. This agreement with our results is remarkable because they emphasized endemism in more inland maritime areas, whereas we emphasized sudden change in total species composition of an extreme maritime habitat.

In contrast to the high regional endemism of the adjacent inland flora, the Dry Mediterranean zone is anomalous, its only unique taxon is *Camissonia cheiranthifolia* ssp. *suffruticosa*. In lacking a unique floristic element and in its total number of species, the Dry Mediterranean zone is analogous to the Subarctic zone.

Within the Dry Mediterranean zone, rainfall declines from 426 mm at Morro Bay ($35^{\circ}20'N$) to 334 mm at Avalon ($33^{\circ}21'N$). An equal drop occurs between Avalon and San Diego ($32^{\circ}44'N$). The flora also shows a decline: four species are lost between 35° and $32^{\circ}30'N$, while at $32^{\circ}N$ a marked floristic shift occurs with three species reaching a southern limit and four a northern one ($K = 0.875$ for $32^{\circ}30' - 32^{\circ}N$, Table 3).

The sharp boundary formed at $32^{\circ}N$ is to the north of any other floristic, climatic, or ecological boundary. Epling and Lewis (1942) considered the adjacent inland region to be the center of the Coastal Sage and Southern Coastal Chaparral communities. The southern boundary of both Howell's (1957) California flora province and Van Dyke's (1919, 1929) California faunal area is much further south (ca $30^{\circ}30'N$). Shreve (1936) considered the same boundary to be the northern limit for the Sonoran Desert in western Baja California. Johnson (1973) found that Baja California dune vegetation also showed a floristic shift near $30^{\circ}30'N$. North of this, *Abronia maritima* is the main beach species, with *Atriplex leucophylla*, *Suaeda californica*, and *Cakile maritima* its most common associates. South of this, *Cakile* and *Ambrosia chamissonis* drop out, and *Sesuvium verrucosum* becomes as prominent as *Abronia*. This major boundary (at $30^{\circ}30'N$) coincides roughly with the change from a semi-arid (BS) to an arid (BW) climate type near $30^{\circ}N$ latitude.

A similar discrepancy appears to occur between the beach and inland flora in the boundary between the Northern and Southern Arid zones. At Punta Abreojos ($26^{\circ}30'N$), the climate changes from a BWk to a BWb type due to the increasing mean annual temperature, which in

effect increases aridity. The coastal boundary between the Viscaino and Magdalena deserts occurs approximately 20' to the south at Bahia San Juanico. Yet the shift from the Northern Arid to Southern Arid beach flora is found several degrees to the north at 28°30'N, near Punta Rosarita.

Likewise, the southern limits of the Southern Arid zone at 24°N near Puerto Magdalena is north of Shreve and Wiggins' (1964) southern limit for the Magdalena desert near Todos Santos at 23°30'N.

Thus, in the more xeric latitudes there is an obvious northward shift in the beach flora when compared to the adjacent inland flora. This suggests that, despite a cooler, maritime climate, the beach is a more extreme habitat than inland habitats in a regional Bs or BW climate.

The beaches here may also be more saline. The floras of the two Arid zones are dominated by Inland-Maritime species, the majority of which are found in saline or alkaline situations inland. In all, there is a total of nine Endemic and Widespread Inland-Maritime species, accounting for 64 percent of the Northern Arid zone's flora and 54 percent of the flora of the Southern Arid zone. Only two of these (*Heliotropium curassavicum*, *Atriplex leucophylla*) extend out of the Arid region. High incidence of otherwise inland halophytes and occurrence of typically salt marsh species such as *Distichlis spicata* and *Suaeda californica*, combined with the northward shift of the Arid zones' boundaries, suggests that the reduction in rainfall has reduced the rate of leaching and created a more saline soil than on beaches to the north.

We consider the region between 24° and 23°30'N to be an ecotone between the Southern Arid and Tropical zones. However, unlike most ecotones, the beach flora between Puerto Magdalena and Todos Santos is depauperate and shows a low degree of similarity to either adjacent zone. *Abronia* and *Sesuvium* continue as the dominant foredune builders until north of Todos Santos (23°30'N), where *Jouvea pilosa* and *Sporobolus virginicus*, two grasses, become dominant. Altogether at Todos Santos about ten beach and dune species make their first appearance and continue south around the cape. Many of the added taxa are pantropical (*Ipomoea*, *Scaevola*). Shreve and Wiggins (1964) and Johnson (1973) point out that this rapid coastal change is paralleled by inland change, from Magdalena desert (low scrub with *Larrea*, *Prosopis*, *Fouquieria*, *Encelia*) to cape thorn forest (woodland with *Lysiloma*, *Cercidium*, *Bursera*).

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VASCULAR PLANTS ON A SPRUCE BALD IN COLORADO

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At Boreas Pass, just below tree-line on the Continental Divide, Summit County, Colorado (39° 25' N, 105° 58' W; 3,609-3,657 m elevation), there is a 90-year-old spruce bald. This bald was formed primarily by clear cutting practices carried out by the Denver, South Park, and Pacific Railroad in its construction of a line over Boreas Pass in 1882 (*Montezuma Millrun*, 1882). Fire has been a secondary influence in forming the bald (Ubbelohde, 1965; E. J. Haley, pers. comm., 1972).

The summit of the pass and the slopes approaching the summit comprise the bald. The area as a whole provides a mosaic configuration of unaltered sites, severely altered sites, and sites of intermediate disturbance among which comparisons of environmental changes may be made. A study of these differences indicates that the major factor controlling vegetation is substrate instability (Olgeirson, 1972). This feature has also been described as a determining factor in arctic vegetation (Raup, 1951; Sigafos, 1952).

Maintenance of the bald is due to the unfavorable influence of a drastically altered environment on tree reestablishment (Stahelin, 1943; Billings and Mark, 1957; Billings, 1969; Olgeirson, 1972). Environmental changes have also created a marked reorientation in herbaceous plant communities. Functionally, this change is regressional, marked by a trend toward vegetation having a physiognomy like alpine fell-fields; floristically, there is a trend toward increased frequency of vascular plants usually associated with the alpine tundra (Billings, 1957, 1969; Weber and Willard, 1967).

Contrasted to this trend are vegetation sites that are unaltered or intermediate. Intermediate sites have been cut-over, usually to a lesser degree than disturbed sites, and operate under environmental conditions that are less inclement. Vegetation shows a mixture of alpine and subalpine physiognomies and flora.

The stable sites are those where no cutting was done. The vegetation dynamics and the flora of these meadows is subalpine in character. The stable sites are floristically diverse; vegetation forms a dense surface cover; soils are deep and relatively fertile; and there is little directional response to physical processes such as wind and snow blast, snow blow-out, run-off, and soil-frost activity. Disturbed sites are floristically poor in comparison; individual taxa have low densities; surface plant cover is very sparse; soils are low in organic carbon—buried soils are the rule due to heavy erosion of surface materials; and there is a strong directional and regressional trend caused by the effects of wind (and associated particles) stress to the surface and vegetation, extreme diurnal temperature variations, snow blow-out, and congelturbation. Intermediate sites have a mixture of the above characteristics (with the exception of frequent pocket gopher activity), although individual sites may be more or less like stable or disturbed sites.

Development of fell-field characteristics by sites on the bald is a response to disturbance. Disturbance has set up process features that parallel those of alpine fell-field situations. The most outstanding floristic changes between disturbed sites and undisturbed sites are in morphology and life form. There is an increase in taxa expressing characteristics that are associated with alpine plants, such as extensive root development and caespitose habit. Conversely, there is a decrease in taxa that are rhizomatous. Life form differences for disturbed and undisturbed sites generally correspond to the differences between alpine and subalpine vegetation (Daubenmire, 1968); there is a predominance of hemicryptophytes and chamaephytes on disturbed sites and a low frequency of phanerophytes, geophytes, and thermophytes on these sites. Conversely, there are higher frequencies of geophytes, phanerophytes, and thermophytes on undisturbed sites and lower frequencies of chamaephytes and hemicryptophytes on these sites (Braun-Blanquet, 1972).

The dominant influences of soil instability on the vegetation of disturbed and intermediate sites are: (1) the maintenance of grasses, especially bunchgrasses (*Festuca ovina*, *Trisetum spicatum*, *Stipa columbiana*, *Agropyron trachycaulum*, *Poa interior*, *P. fendleriana*, and *Deschampsia caespitosa*) and tussock forming sedges (*Carex chalciolepis* and *C. epapillosa*); (2) the increased occurrence of weedy and ubiquitous forbs (*Achillea lanulosa*, *Chrysopsis villosa*, *Senecio werneriaefolius*, *Antennaria parvifolia*, *Cirsium parryi*, *Taraxacum officinale*, *Tragopogon pratensis*, *Penstemon whippleanus*, *Chenopodium leptophyllum*, *Arabis drummondii*, and *Phacelia sericea*); and (3) the introduction of plants

more strictly associated with the alpine tundra or of plants having morphological characteristics common to alpine plants (*Geum rossii*, *G. triflorum*, *Bistorta bistortoides*, *B. viviparum*, *Sibbaldia procumbens*, *Oreoxis alpina*, *Eritrichium aretioides*, *Mertensia alpina*, *Androsace septentrionalis*, *Oxytropis parryi*, *Delphinium alpestre*, *Sedum lanceolatum*, *Lewisia pygmaea*, *Draba exunguiculata*, *Polemonium viscosum*, *Minuartia macrantha*, *M. obtusiloba*, *Townsendia rothrockii*, *Artemisia patersonii*, *A. scopulorum*, *Erysimum nivale*, *Erigeron simplex*, *Luzula spicata*, *Lloydia serotina*, *Ranunculus adoneus*, *Saxifraga serpyllifolia*, *Pedicularis parryi*, and *Chaenactis alpina* var. *leucopsis*, as well as the grasses and other taxa included above). Intermediate soil instability is also reflected by the occurrence of putative hybrids, such as *Potentilla concinna* (W. Weber, pers. comm., 1972).

Contrasted to the predominance of the above taxa, and the morphologies that they represent, is the decreased frequency of rhizomatous taxa such as *Carex foenea* and *Juncus drummondii*, and the absence of other taxa previously associated with *Carex foenea* sods (*Veronica wormskjoldii*, *Erigeron speciosus*, and *E. glabellus*) and with moist subalpine meadows (*Trifolium parryi*, *Arnica cordifolia*, *Antennaria anaphaloides*, *Thlaspi alpestre*, *Gentiana calycosa*, *Carex hoodii*, *C. nelsonii*, *Potentilla diversifolia*, *Fragaria vesca* ssp. *americana*, *Poa alpina*, *Ranunculus inamoenus*, *Castilleja sulphurea*, *Anemone narcissiflora* ssp. *zephyra*, *Agrostis thurberiana*, *Astragalus alpinus*, *Campanula parryi*, *Oxytropis lambertii*, *Senecio crocatus*, *Mertensia bakeri*, *Gentianopsis thermalis*, *Swertia perennis*, *Allium rubrum*, *Penstemon procerus*, *Valeriana capitata*, and *Erigeron subtrinervis*).

The physiognomy and flora of the disturbed sites at Boreas Pass reinforces the idea that the difference in adaptive abilities in alpine and subalpine vascular plants is a measure of specific tolerances. The one tolerance most applicable here is that of cyclic phenomena of a harsh or disruptive nature, such as soil instability.

The following sources were used in the identification of plants: Hitchcock (1950); Harrington (1954); Taylor (1959); Murray (1969); Weber (1972); and Å. Löve, pers. comm. (1972). A checklist of all species found at Boreas Pass, indicating their occurrence on disturbed, intermediate, or undisturbed sites, is available from the author on request. Vouchers are in the herbarium of the University of Colorado, Boulder (COLO). My thanks go to Áskell Löve for his help in identifying certain taxa and to Miriam Colson for her aid in identifying sedges.

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NEW OR INTERESTING SPECIES OF CLAUDOPUS AND ENTOLOMA FROM THE PACIFIC COAST

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A survey of the rhodophylloid fungi sensu Largent and Benedict (1971) found on the Pacific Coast of the United States has been underway since late 1960. Type specimens of those species described as new from this area have been studied and a report published (Largent, 1971). A list of species previously reported from California, Washington, and Oregon, as well as descriptions of various taxa of *Nolanea*, were published in 1972 (Largent and Thiers, 1972). Additionally a study of *Alboleptonia* was completed and included several species from the Pacific Coast (Largent and Benedict, 1970).

The following account describes my studies of *Claudopus byssisedus* and is the first report of this species from Washington and California. Also included in this report are the following: the first report of *Entoloma madidum* from Washington; a description of a previously undescribed form, *E. madidum* var. *madidum* f. *jarinosum*; the creation of a

new variety, *E. madidum* var. *bloxamii*, having as its basionym, *Agaricus bloxamii*; and a discussion and descriptions of a new species *Entoloma trachyosporum* and two new varieties, *E. trachyosporum* var. *griseoviolaceum* and var. *purpureoviolaceum*.

Chemical formulas and techniques for making macrochemical tests are to be found in Largent and Benedict (1970) with the abbreviation of PDAB being used for *p*-Dimethylaminobenzaldehyde. Measurements were made from 10–14 spores, basidia, or cystidia and did not include the apiculus of the basidiospores or the sterigmata of the basidia. Abbreviations used in the taxonomic descriptions are as follows: L = length, D = diameter, L/D = length divided by the diameter, L–D = length minus diameter. The colors used in the descriptions are from Konerup and Wanscher (1961). For example (6, A, 2–3) indicates the page, row, and column, respectively. Unless cited otherwise, *L* preceding the collection number or list of numbers indicates the collections are mine. All collections are deposited in the cryptogamic herbarium of CSU–Humboldt (HSC).

1. CLAUDOPUS BYSSISEDUS (Pers. ex Fr.) Gill., Champ. Fr. 427. 1876.

Pileus 7–35 mm broad, dimidiate to reniform, at times sessile, concave or effuso-reflexed; surface glabrous and greyish orange to brownish orange (5–7, B–C, 2–4) beneath a dense layer of whitish fibrils; margin inrolled to incurved, entire and faintly translucent-striate at first becoming decurved, eroded, and non-translucent with age; smooth to undulating; context up to 2 mm thick, light greyish brown, unchanging on bruising; odor and taste farinaceous. Lamellae adnate to uncinata, subdistant, narrow, 2–3.5 mm wide, 10–15 mm long, pallid to light greyish brown becoming pinkish with spore maturation; margin smooth, concolorous, unchanging when bruised. Stipe 1–2 mm broad at the apex, 2–3 (–5) mm long, eccentric to lateral and decidedly curved, at times absent; basal portion of stipe protruding from a dense whitish mycelial mat that forms the fibrils on the pileus; white rhizomorphs radiate throughout the substrate and are attached to the mycelial mat.

Spores $8.0\text{--}10.0 \times 6.5\text{--}7 \mu\text{m}$, average length $8.9 \mu\text{m}$, average width $6.8 \mu\text{m}$, L–D $0.5\text{--}3.0 \mu\text{m}$ (average $2.1 \mu\text{m}$), 5–6 -sided, elongate angular; basidia clavate, $34\text{--}44 \times 9\text{--}12 \mu\text{m}$, average length $37.5 \mu\text{m}$, average width $10.2 \mu\text{m}$, L/D $3.4\text{--}4.0$ (average 3.6), 2–4 spored; cheilocystidia rare to scattered, versiform, $50\text{--}55 \times 7.5\text{--}10.0 \times 5\text{--}7$ (apex) μm ; pleurocystidia absent; pileal cuticle an undifferentiated epicutis, 1–2 cells thick, hyphae parallel to the hyphae of the pileal trama; epicutis overlain with a layer of loosely interwoven hyphae, the terminal cells of which are versiform in shape and measure $28\text{--}42$ (–100) $\times 9\text{--}12 \times 5\text{--}6$ (apex) μm , average length $38 \mu\text{m}$, average width $10.6 \mu\text{m}$, L/D $3.1\text{--}4.2$ (average 3.6); pileal trama homogeneous; subhymenium irregular and obscure; cuticle at the stipe apex a palisade trichodermium, at times covered by a superficial layer of hyphae; caulocystidia versi-

form, $37.5\text{--}107.5 \times 4\text{--}17 \times 2.5\text{--}6.0$ (apex) μm , average length 71.1 μm , average width 8.0 μm , average width (apex) 7.5 μm , L/D 4.4–20.5, average 8.9. Clamp connections abundant, present on the hyphae of the superficial layer, of the pileal cuticle, of the cuticle at the apex of the stipe, of the basal mycelial mat, of the rhizomorphs and at the base of the basidia. Pigmentation vacuolar.

Macrochemical reactions: Guaiac, guaiacol, pyrogallol, alpha-naphthol, PDAB positive; aniline, phenol, sulphuric acid, sulfovanillin, Melzer's, selenium dioxide negative.

Habitat and Distribution: On the underside of various substrata: moss mats, rotting conifer and oak branches and logs, and in the crevices of redwood stumps. California and Washington.

Material Studied: CALIFORNIA. Humboldt Co.: L5280, 5496, 5497. WASHINGTON. King Co.: L1699; Mason Co.: L2021; Pierce Co.: L1059; San Juan Co.: L1482, 2043; Snohomish Co.: L1602.

Claudopus byssisedus is easily recognized by its greyish brown lamellae, greyish brown pileus beneath a dense whitish veil, villose stipe, white rhizomorphs, mealy odor and elongate spores that measure $8\text{--}10 \times 6\text{--}7 \mu\text{m}$. My specimens are quite similar to descriptions given for *C. byssisedus* by Fries (1821), particularly the color of the pileus and stipe, and the byssoidal fibrils (rhizomorphs) at the base of the stipe. Fries makes no comments on odor or taste.

Rhodophyllus byssisedus (Fr.) Quél. sensu Kühner and Romagnesi (1953) differs from my specimens by having an incrusting pigmentation albeit minute (p. 182) and no clamp connections on the hyphae. Kühner and Romagnesi mention nothing about a villose stipe or about basal rhizomorphs; however they state Fries considered *C. byssisedus* to have a stipe surrounded at the base with byssoidal white fibrils. Since they accepted Fries' concept of this species, one wonders whether their specimens had all of the Friesian features or just the ones mentioned in their description.

Entoloma byssisedum (Fr.) Donk sensu Hesler (1967) differs from all concepts of *C. byssisedus* heretofore mentioned because of its white lamellae, absence of veil on the pileal surface, absence of a villose stipe, absence of rhizomorphs, absence of clamp connections, and having a mild odor. *Rhodophyllus byssisedus* sensu Lange (1936) differs by having pallid gills; no mention is made of the stipe surface, basal rhizomorphs, odor, or taste. *Rhodophyllus undatus* (Fr.) Quél sensu Kühner and Romagnesi (1953) and *Entoloma depluens* (Fr.) Hesler (1967) differ from my concept of *Claudopus byssisedus*—the former because of its consistently centrally attached stipe, pale whitish fibrils on the pileal margin, glabrous pileal disc, glabrous stipe, incrusting pigmentation and lack of rhizomorphs, the latter because of its broader spores ($7\text{--}8 \mu\text{m}$), mild odor and lack of cheilocystidia and rhizomorphs.

On the Pacific Coast, *Claudopus byssisedus* was previously reported only from Mt. Hood, Oregon (Kauffman, 1925).

2. *Entoloma madidum* (Fr.) Gill., Champ. Fr. 399. 1876. var. *MADIDUM* forma *MADIDUM*.

Basionym: *Agaricus madidus* Fr., Epicrisis 144. 1838. for similar species, see the discussion of *Entoloma madidum* var. *madidum* f. *farinosum*.

3. *Entoloma madidum* (Fr.) Gill., Champ. Fr. 399. 1876. var. **madidum** f. **farinosum** Largent, f. nov.

Ut in typo sed odor et sapor farinacei.

Pileus 35–100 mm broad, 10–17 mm high, convex to broadly convex at first, becoming plane and finally uplifted with age, at times obscurely to broadly umbonate; surface glabrous, lubricous to slippery from a partially gelatinized cuticle, at times viscid, often rugulose; bluish gray to dark blue (19–23, F, 2–3(–4)) becoming orange-white (5–6, A, 2) in areas covered by leaves and debris; margin rugulosely striate, often to the disc, even and decurved; trama 7–17 mm thick, white with a decided bluish tinge on exposure to air; odor and taste farinaceous. Lamellae sinuate to emarginate, moderately broad to broad, sigmoid to ventricose, close becoming subdistant with age, 3.5–11.0 mm broad, 15–35 mm long, white at first becoming pinkish with spore maturation; margin concolorous, smooth at first becoming eroded with age. Stipe equal to tapering from apex to base, often widest in the middle, 11–30 mm wide at the apex, 16–24 mm wide in the middle, 9–19 mm wide at the base, 50–110 mm long; surface interwoven fibrillose, the fibrils often irregularly agglutinated and then the surface rimose, bicolorous, bluish grey to dull blue (21–23, D–F, 2–5) at apical one-third to two-thirds at first yellowish white to orange-white becoming, with age and handling, pale yellow, pale orange, or light orange (4–5(–6), A, 2–3 to 4–5(–6), A, (2–)3–4) at the base, frequently white to bluish white to bluish grey in those apical areas unexposed to light (either covered by leaves and debris or between fibrils and in rimose areas); trama concolorous with pileal trama.

Spores $6.5\text{--}8.5 \times 6.0\text{--}8.0 \mu\text{m}$, average length $7.8 \mu\text{m}$, average width $7.5 \mu\text{m}$, L–D $0.0\text{--}1.5 \mu\text{m}$ (average $0.3 \mu\text{m}$), ovate angular, at times almost angular nodulose; basidia $37\text{--}50 \times 10\text{--}12 \mu\text{m}$, average length $42.8 \mu\text{m}$, average width $11.1 \mu\text{m}$, L/D 3.8–4.2 (average 3.9), 4-spored clavate; subhymenium indistinct; cheilocystidia and pleurocystidia absent; pileal cuticle a distinct gelatinous epicutis with the hyphae interwoven, slightly gelatinized and $3.8\text{--}7.5 \mu\text{m}$ wide; at times debris abundant on the pileal cuticle; hypoderm indistinct; stipe cuticle an undifferentiated epicutis of repent hyphae; caulocystidia absent; lactifers rare in the pileal trama, scattered in the stipe trama; pigmentation vacuolar; clamp connections abundant on the hyphae of the pileal cuticle and at the base of the basidia.

Macrochemical reactions: Guaiac, guaiacol, pyrogallol, and alpha-naphthol positive on the pileal flesh just above the lamellae, lamellar

surface, and the pileal and stipe surfaces, negative elsewhere; selenium dioxide, sulfovanillin, KOH, and sulphuric acid questionable; aniline, phenol-aniline, thallium oxide, and PDAB negative.

Habitat and Distribution: Scattered to gregarious and at times solitary in humus of dense mixed woods, coniferous woods and mixed conifer-redwood forests; collected beneath mountain hemlock, western red cedar, Douglas fir, and at times near redwood; Washington and California.

Type: Solitary in needle humus of coniferous woods, near western red cedar, Sulphur Creek campground, Mt. Baker National Forest, Snohomish Co., Washington; 17 Oct 1966; *Largent 1849* (HSC).

Material Studied: CALIFORNIA. Del Norte Co.: *L4029, 4030, 4031, 4032, 4033, 4034, 5224*. Humboldt Co.: *Thiers 14565*. Marin Co.: *Mad-den 847; Thiers 18140; L810, 812*. Mendocino Co.: *Thiers 14642, 18402, 21325; L791, 5434*. San Mateo Co.: *Thiers 8687, 12188, 12203, 18333; L807*. Santa Cruz Co.: *Thiers 13537*. Sonoma Co.: *L4215*. WASHINGTON. Jefferson Co.: *L3150*. Kittitas Co.: *L1319*. Pierce Co.: *L1358*. Snohomish Co.: *L1296, 1849, 3232*.

Entoloma madidum is easily recognized by its tricholomatoid habit, viscid to lubricous pileal surface, blue to bluish grey pileus and stipe apex, eventual yellowish tinged stipe base, white lamellae when young, and mealy odor. With the exception of the forms with a consistent white stipe base, my specimens seem to agree with Hesler's concept (1967, p. 112) of this species.

Entoloma bloxamii (Berk. & Br.) Sacc. is similar to *Entoloma madidum* because of its blackish blue pileus, yellowish white stipe base, and slightly mealy odor but differs by having spores 8–10 μm long. *Entoloma bloxamii* has been considered a form of *Rhodophyllus madidus* (Fr.) Quél. (= *Entoloma madidum*) by Kühner and Romagnesi (1953). In addition, Kühner and Romagnesi comment on collecting specimens with smaller spores and a mealy odor (no mention of stipe base color is made) intermediate between *Entoloma bloxamii* and *Rhodophyllus madidus*. In their description of *R. madidus* (p. 197) no mention is made of a viscid or lubricous pileus, nor of a yellowish stipe base although they do state the stipe base is definitely not greyish blue or slate violet.

The color of the stipe base in my specimens is variable, at first white and becoming yellowish with age and/or handling; therefore, this feature is considered taxonomically insignificant. However, no variation was noted in spore size or in odor; consequently these features appear stable and should receive some emphasis in the taxonomy of *Entoloma madidum*. I agree with Kühner and Romagnesi that *E. bloxamii* is a form of *E. madidum*, but I feel the two taxa should be separated on the basis of spore size. Thus, two varieties of *E. madidum* are proposed: 1) variety *bloxamii* for those specimens with large spores (8–10 μm) based upon *Agaricus bloxamii* Berk. & Br., and 2) variety *madidum* for those specimens with smaller spores (6–8 μm) based upon *Agaricus madidus* Fr.

Two new forms are proposed for this latter variety: 1) *E. madidum* var. *madidum* forma *madidum* for those specimens with a foetid odor, like *Russula foetens*, based on Fries' original concept of *Agaricus madidus*, and 2) *E. madidum* var. *madidum* forma *farinosum* for specimens with a mealy odor. My specimens, Hesler's specimens, and at least the intermediate forms of Kühner and Romagnesi belong to the latter form.

Entoloma nitidum sensu Kühner & Romagnesi is similar to *E. madidum* var. *madidum* forma *farinosum* because of its bluish color but differs by having a more slender stipe, a raphanoid-herbaceous taste and larger spores.

Entoloma madidum was reported previously from the West Coast only from San Rafael, California (Harkness and Moore, 1880).

4. **Entoloma madidum** (Fr.) Gill. var. **bloxamii** (Berk. & Br.) Largent, comb. et stat. nov.

Basionym: *Agaricus bloxamii* Berk. & Br. Outlines, p. 143. 1860. For a discussion of similar species, see entry No. 3.

5. **Entoloma** (Fr.) Kummer emend. Largent & Benedict sect. **Turfosi** (Kühner & Romagnesi) Largent, comb. et stat. nov.

Basionym: *Rhodophyllus* Quél. subg. *Entoloma* Fr. sect. *Nolanidei* Fr. group *Turfosi* Kühner & Romagnesi, Flore Anal. des Champ. Supérieurs, p. 196. 1953.

6. **Entoloma** (Fr.) Kummer emend. Largent & Benedict sect. **Turfosi** (Kühner & Romagnesi) Largent subsect. **Trachyosporum** Largent, subsect. nov.

Pileus et stipes lubrici; sporae $6.0-8.5(-9.0) \times 5.5-7.0(-8.0) \mu\text{m}$, ovato-angulatae et obscurae angulatae. Typus: *Entoloma trachyosporum* Largent.

Because of the small spores with inconspicuous angles, pilei not exceeding 6 cm in diameter, their mild to raphanoid odor, vacuolar pigmentation and abundant clamp connections, species of this subsection appear to belong to group *Turfosi*, section *Nolanidei*, subgenus *Entoloma* sensu Kühner & Romagnesi. In my opinion, this set of features, particularly the spores and the small pileal size, is sufficiently significant to raise this group to sectional rank.

The subsection *Trachyosporum* is monotypic. *Entoloma trachyosporum* has three color variants, differing from one another by the amount of violaceous to purplish pigment present in the carpophore. Correlated with these pigment differences is a distinct gradation in macrochemical reactions. Variety *trachyosporum* has no violaceous or purplish color and does not react macroscopically with any reagents; var. *griseoviolaceum* has a violaceous stipe and the pileal flesh reacts with alpha-naphthol; and var. *purpureoviolaceum* has a violaceous stipe, a brown pileus with a

reddish to purplish tinge, and reacts positively with pyrogallol and selenium dioxide but not with any other reagents.

KEY TO VARIETIES OF *E. trachyosporum*

Stipe white to pallid, often darkening with age; pileus at first greyish brown, becoming paler with age var. *trachyosporum*.

Stipe and pileus not as above

Pileus purplish brown to reddish brown at first; lamellae bluish grey when young; pileal flesh purplish blue to violaceous grey

. var. *purpureoviolaceum*.

Pileus grey brown, at least on the disc; lamellae pallid to greyish brown when young; pileal flesh buff . . . var. *griseoviolaceum*.

7. *Entoloma trachyosporum* Largent, sp. nov.

Pileus 13–40 mm latus, convexus, glaber lubricus et plus minusve subviscidus, hygrophanus, griseolo-brunneus vel vulvus fuscus; contextus pilei aurantio-albus; lamellae adnexae vel sinuatae, pallidae vel subalbae primo; stipes 2–7 mm crassus, 30–90 mm longus, lubricus, appressofibrillosus vel glaber, subalbus demum aurantio-griseus vel brunneolo-aurantius; sporae $6.0\text{--}8.0 \times 5.5\text{--}7.0 \mu\text{m}$, verrucoso, angulatae; cystidia nulla; hyphae cutis filamentosae, repentes.

Pileus 13–40 mm broad, 4–12 mm high, convex, at times almost parabolic becoming broadly convex to plane with age, often acutely to broadly umbonate; surface glabrous, lubricous and more or less subviscid, hygrophanous; at first greyish brown or dark yellowish brown to dark brown (5–6, E–F, 3–5), remaining so on the disc but elsewhere becoming brownish orange to light greyish brown or greyish orange (5–6, B–D, 3–5), at times even as light as orange-grey (5, B, 2); margin decurved and entire, with age becoming plane, and at times eroded, translucent-striate when moist, becoming nontranslucent with age; trama orangish white (6, A, 2), 2–4 mm wide on the disc, taste and odor mostly indistinct, at times faintly raphanoid. Lamellae finely adnexed with a decurrent tooth to sinuate, subdistant, narrow to moderately broad, at times almost broad, 2–7 mm wide, 5–15 mm long, pallid to an off-white at first; margin smooth becoming eroded, concolorous with surface. Stipe 2–7 mm wide at the apex, 4–10 mm wide at the base 30–90 mm long, equal to more or less clavate, lubricous, silky appressed fibrillose to glabrous, longitudinally striate, the surface hyphae agglutinated with age making the surface irregular rimulose, at first an off-white (6, A–B, 1) becoming orange-grey to brownish orange (5–6, A–D, 2–5) and rarely dark yellowish brown (5, E–F, 5) with age and on handling; trama concolorous with the pileus, fleshy-fibrous, basal tomentum scant to absent.

Spores $6.0\text{--}8.0 \times 5.5\text{--}7 \mu\text{m}$, average length $7.1 \mu\text{m}$, average width $6.2 \mu\text{m}$, L–D 0.0–1 (–2.0) μm (average $0.9 \mu\text{m}$), 6–8 angled, ovate and warty angular, almost *Rhodocybe*-like but definitely angular in end

view; basidia $30-39 \times 7.5-9.0 \mu\text{m}$, average length $34.6 \mu\text{m}$, average width $8.3 \mu\text{m}$, 4-spored, clavate; cheilocystidia and pleurocystidia absent; pileal cuticle a repent layer of filamentous hyphae with terminal cells cylindro-clavate, $30-67.5 \times 4.0-7.0 \mu\text{m}$, average length $50.0 \mu\text{m}$, average width $5.5 \mu\text{m}$, L/D 5.7-13.9, average 9.9; hypoderm of elliptical to ovate cells; tramal hyphae interwoven; oleiferous hyphae abundant in pileal and stipe trama; pigmentation vacuolar; clamp connections present on hyphae of the pileal and stipe cuticle, at the base of the basidia, and questionable at the base of the stipe.

Macrochemical Reactions: Guaiac, guaiacol, alpha-naphthaol, pyrogallol, PDAB, selenium dioxide, and Melzer's negative.

Habitat and Distribution: Scattered to gregarious in humus of coniferous woods, beneath Douglas fir; Washington.

Type: Scattered to gregarious in mossy humus of a coniferous forest, beneath Douglas fir; southeast of Tenino mounds, Thurston County, Washington; 4 Nov 1966; *Largent 2169* (HSC).

Material Studied: WASHINGTON. Gray's Harbor Co.: *L1961*; King Co.: *L1719, 1865*; Mason Co.: *L2027*; Pierce Co.: *L1187, 1657, 3152*; Snoqualmie Co.: *L2799, 3236*; Thurston Co.: *L2196*.

The greyish brown color of the pileus that becomes yellowish brown on fading, pallid lamellae, whitish stipe at first that darkens with age, and buff color of the pileal flesh are features that characterize *E. trachyosporum*.

8. *Entoloma trachyosporum* Largent var. *griseoviolaceum* Largent, var. nov.

Ut in typo sed pileus griseo-brunneus disco; lamellae pallidae vel griseobrunneae primo; contextus pilei bubalinus; stipes violaceus.

Pileus 13-60 mm broad, 7-15 mm high, convex to broadly convex at first becoming broadly convex to plane, at times broadly umbonate, glabrous and definitely lubricous, slippery to the touch, hygrophanous, at first dark greyish brown (6, F, 2-3), remaining so on the disc, becoming orange-white to pale orange (light brownish) (6, A-C, 2-3(-4)) on the margin; margin decurved becoming plane with age, even, smooth, translucent-striate; trama (2-)3-4 mm thick, pale light brown (6, A-B, 2) at times; odor and taste indistinct. Lamellae uncinata to adnexed, subdistant, narrow to moderately broad, 3-9 mm wide, 8.5-22.0 mm long, grey at first becoming brownish with a pinkish tinge with age. Stipe (3-)4-7 mm wide at the apex, (4-)7-8 mm wide at the base, 35-90 (-100) mm long, equal to more or less clavate, glabrous but with the surface fibrils agglutinated and then the surface interwoven rimulose, hygrophanous, medium greyish violet to dark bluish grey (17-21, D-F, 2-4), fading to silvery violaceous white to pale bluish grey (19-21, A-C, 2-4), basal tomentum area whitish becoming very pale yellowish brown on bruising (5-6, A, 2-3); trama pale violaceous white, fleshy-fibrous, hollow with age.

Spores $6.5-8.0(-10) \times 5.5-7.0(-8.0) \mu\text{m}$, average length $7.0 \mu\text{m}$, average width $6.5 \mu\text{m}$, L-D $0.0-1.5 \mu\text{m}$ (average $0.5 \mu\text{m}$), ovate and warty angular, distinctly angular in end view; basidia $26-32 \times 8.5-10.0 \mu\text{m}$, average length $29.6 \mu\text{m}$, average width $9.6 \mu\text{m}$, 4-spored, clavate; cheilocystidia and pleurocystidia absent; pileal cuticle a loosely interwoven to repent layer of filamentous hyphae the terminal cells of which are cylindro-clavate and measure $47.5-87.5 \times 5.0-6.5 \mu\text{m}$, average length $69.4 \mu\text{m}$, average width $5.6 \mu\text{m}$ L/D $9.5-17.5$ (average 12.3), at times more or less subviscid; hypoderm tightly interwoven; trama homogeneous; cuticle at the stipe apex an undifferentiated epicutis of repent hyphae; caulocystidia absent. Oleiferous hyphae absent; pigmentation vacuolar; clamp connections abundant, present on the hyphae of the pileal cuticle, on the hyphae of the basal tomentum and at the base of the basidia.

Macrochemical Reactions: Alpha-naphthol positive; pyrogallol and selenium dioxide questionable; guaiac, guaiacol, PDAB, and sulfovanillin negative.

Habitat and Distribution: Scattered to gregarious in needle or mossy humus in coniferous forests, collected beneath deer fern, *Trillium* sp., Douglas fir, western red cedar, and hemlock; late September to early November, Washington.

Type: Scattered to gregarious in mossy humus beneath hemlock, Ipsut Lake trail, Mt. Rainier National Park, Clallam Co., Washington, 25 Sept 1966; *Largent 1659* (HSC).

Material Studied: WASHINGTON. Clallam Co.: *L1659*; Pierce Co.: *L1354, 1843*; Snohomish Co.: *L1714, 1867*.

9. *Entoloma trachyosporum* Largent var. *purpureoviolaceum* Largent, var. nov.

Ut in type sed pileus purpureiobrunneus vel rufibrunneus primo; lamellae caesiaae primo; contextus pilei purpureus vel violaceo-griseus; stipes violaceus.

Pileus 13-60 mm broad, 5-18 mm high, convex to parabolic or broadly convex at first becoming broadly convex to plane, at times uplifted, obscurely to broadly umbonate; glabrous, at times more or less minutely velvety on the disc, lubricous and slippery to the touch., more or less subviscid due to apparent gelatinized superficial hyphae, hygrophanous in radial streaks, dark brownish grey with reddish to purplish tinges (9-11, E-F, 2-3) to reddish grey (12, E-F, 2-3) to purplish grey (13-14, E-F, 2-3) becoming on fading brownish grey (6-8, F, 2-3) on the disc and orange-grey to greyish orange (6, B, 2-3) or light reddish grey to greyish red (7, B, 2-3) or light brownish grey to brownish orange (6-7, C, 2-3) on the margin; margin decurved, entire to eroded, smooth and undulate, translucent-striate at first; trama 2-5 mm thick, at first pallid buff (7, C, 3) becoming on exposure to air greyish blue to bluish grey to dark blue (20, D-E, 3-4); taste and odor indistinct, at

times more or less fragrant and pleasant. Lamellae finely adnexed with a decurrent tooth, mostly subdistant to distant but at times crowded to close, moderately broad to broad (2–8 mm wide, 8–15 mm long), grey to bluish grey at first becoming brownish pink with spore maturity; margin smooth and concolorous with the face. Stipe 2.5–5.0 mm wide at the apex, 3.5–8.0 mm wide at the base, 10–90(–120) mm long, equal to more or less clavate; surface more or less gelatinized, longitudinally striate, lubricous to more or less subviscid, surface hyphae often agglutinated and therefore the surface becoming interwoven rimulose, hygrophanous and rippled, at first dark bluish grey (19–23, D–F, 2–3 (–4)), fading from the base upward to a violaceous or bluish white (19–23, A, 2) to a light bluish grey (19–23, B, 2–3) or a greyish violet (19, B, 3); trama fleshy becoming hollow, greyish-violet (18–19, D–F, 3–4); basal tomentum copious, whitish becoming buff tinged (5–6, A, 2) with age.

Spores $5.5\text{--}8.0 \times 5.5\text{--}7.0 \mu\text{m}$, average length $7.0 \mu\text{m}$, average width $6.5 \mu\text{m}$, L–D $0.0\text{--}1.5 \mu\text{m}$ (average $0.5 \mu\text{m}$), ovate to warty angular; basidia $28\text{--}35 \times 7.0\text{--}10.0 \mu\text{m}$, average length $32.0 \mu\text{m}$, average width $8.6 \mu\text{m}$, 4-spored, clavate; cheilocystidia and pleurocystidia absent; pileal cuticle a loosely interwoven layer of more or less gelatinized filamentous hyphae, terminal cells cylindro-clavate, $30\text{--}67.5 \times 4.0\text{--}10.0 \mu\text{m}$, average length $47.5 \mu\text{m}$, average width $7.3 \mu\text{m}$, L/D $5.0\text{--}9.2$ (average 6.4), overlaying a distinct hypodermal area of clavate to ovoid hyphae; trama interwoven; cuticle at the stipe apex an undifferentiated epicutis of repent hyphae. Lactifers abundant in the pileal and stipe tramas; clamp connections abundant on the hyphae of the pileal cuticle and at the base of the basidia, scattered on the hyphae of the stipe cuticle and basal tomentum; pigmentation vacuolar.

Macrochemical Reactions: Pyrogallol and selenium dioxide positive; alphanaphthol, guaiac, guaiacol, sulfovanillin, and Melzer's negative.

Habitat and Distribution: Scattered to gregarious in needle or mossy humus of coniferous forests, early September to late November; Washington.

Type: Scattered in mossy humus of coniferous forests, collected beneath western red cedar; two miles southwest of Troublesome campground, Snoqualmie National Forest, Snohomish Co., Washington; 5 Nov 1966, *Largent 2197* (HSC).

Material Studied: WASHINGTON. Gray's Harbor Co.: *L1960*; King Co.: *L1302, 2028*; Kitsap Co.: *L2259*; Mason Co.: *L2092, 2145*; Pierce Co.: *L1675, 3151*; Snohomish Co.: *L1695, 2197, 2806, 3230*.

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EUPHORBIA (SUBG. AGALOMA) HENRICKSONII, NEW SPECIES FROM THE CHIHUAHUAN DESERT

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The extensive and increasingly accessible arid areas of north-central Mexico have yielded a number of interesting new taxa in our explorations designed to supply the materials for a *Chihuahuan Desert Flora*. The handsome species described here is strikingly distinct from any heretofore described. I am happy to associate with it the name of Dr. James S. Henrickson, California State University—Los Angeles, an able and extraordinarily enthusiastic worker who, with considerable personal sacrifice, has mounted a strenuous collecting campaign and is collaborating in the production of the manual flora.

Euphorbia henricksonii, sp. nov. Herbae annuae erectae 5–35 cm altae; caulis infime 2–5 mm crassis; rami oppositi vel pseudodichotomi pubescentes; laminae foliorum elliptico-oblancoolatae 0.8–2.5 cm longae integrae fere glabrae; petioli 2–7 mm long; cyathia obpyramidalia vel hemisphaerica 1.7–2.0 mm longa pedunculis 2–3 mm longis; glandes 5 oblongae 0.8–1.0 mm longae; appendices 5 petaloideae orbiculares albae 1.7–3.0 mm longae lataeque; flores staminati 30–35; styli 3 basi bifurcati 1 mm longi; capsulae 2.7–3.0 mm longae; semina 2.4–2.5 mm longa microtuberculata.

Annual taprooted gray-green herbs (5–) 10–25 (–35) cm tall, at base with a single stem 2–5 mm thick and with few to numerous ascending opposite branches or often at some nodes pseudodichotomous (the main axis bearing a terminal cyathium, the subsequent overtopping growth emerging from the axils of the opposite leaves), the internodes sparsely and the nodes more densely pubescent with whitish hairs 0.1–0.2 mm long. Leaves opposite; blades elliptic-oblancoolate, (0.8–) 1.5–2.0 (–2.5) cm long, (3–) 5–7 (–10) mm wide, at apex rounded or bluntly acute, at base cuneate, marginally entire, above glabrous, beneath sparsely pubescent with curved whitish hairs 0.1–0.2 mm long; petioles very slender (2–) 3–5 (–7) mm long, pubescent. Cyathia early in the season terminal in the forks of the pseudodichotomous branches, later more congested in cymose arrangements at the top of the plant; peduncles 2–3 mm long; cyathia obpyramidal to hemispherical, 1.7–2.0 mm long to base of glands, olive-green, sparsely pubescent with whitish spreading hairs 0.2–0.3 mm long; glands 5, oblong, 0.8–1.0 mm long (measured parallel to the cyathium-rim), 0.5 mm wide, olive-yellow, medially with a shallow groove; petaloid appendages 5, white, roughly orbicular, 1.7–3.0 mm long and wide, often a little wider than long, above glabrous, beneath sparsely pubescent with whitish hairs 0.1–0.2 mm long; staminate flowers 30–35; pistillate flower exserted about 3 mm above top of cyathium; styles 3, 1 mm long, each bifurcate to the base, the divisions filiform; capsule 2.7–3.0 mm long, slightly thicker than long, glabrous; seed essentially ecarunculate, ovoid, 2.4–2.5 mm long, 1.8 mm thick (dry) or 2.0 mm thick moistened (measured tangentially), 1.5 (dry) or 1.7 (moistened) mm thick from dorsum to venter; inner coat tough, nearly smooth, dark brown; outer coat of variable thickness, grayish, white, hydrophilic, uniformly and closely tuberculate, the tubercles about 0.1 mm long and thick.

TYPE: Mexico, Chihuahua, Bajío El Gringo, 27°48'N lat, 104°52'W long, 1275 m elev., 29 Sep 1972, *M. C. Johnston, F. Chiang, and T. L. Wendt 9585* (holotype, TEX; isotypes to be distributed, MEXU, RSA, and elsewhere).

The type and only known locality is along the relatively new "highway" traversing eastern Chihuahua from Ojinaga south through the La Perla mining district. Only 26 km from its southern terminus (junction

with the Ciudad Camargo-Jimenez highway) the road crosses the flat bottom of an internal drainage basin, Bajio El Gringo, in which the soil is a finely-textured, slightly alkaline and mineralized adobe and the vegetation consists mainly of large clumps of alkali zacaton, *Sporobolus airoides* (Torr.) Torr. Although I have traversed this region several times, only once, at the end of the summer rainy season of 1972, have I been in this locality when the ground seemed moist enough and the vegetation in active enough growth to warrant stopping for botanical sampling. The flora is of limited interest except for the present species. Several hundred thousand plants of it were seen in a very local area, along both sides of the highway, in ditches that had been gouged by road-machinery scarcely a year and a half before. In contrast to its abundance in this devastated (but only lightly grazed) habitat where competing vegetation was essentially absent, *E. henricksonii* was scarce in the less mechanically disturbed but heavily grazed zacatonal across the fence. We have found it nowhere else in hundreds of miles of seemingly similar alkali flats elsewhere in the desert and consider it rare. Some of our specimens show grazing injury.

A search for a close relative of *E. henricksonii* has been unsuccessful. The species is obviously, on the basis of the obsolete stipules and cythial traits, a member of subgenus *Agaloma* (Raf.) House as broadly defined by recent authors. But there the trail ends. The relatively large pubescent cyathia with showy appendages and obsolete caruncles are reminiscent of the group of species (*E. torrida* L. and relatives) with bicolored bracts, but the phyllotaxy, branching pattern, and seed-coat texture seem to rule out any close relationship. The closest relatives may be some slender herbs including *E. bifurcata* Engelm. and *E. exstipulata* Engelm. but again phyllotaxy, branching pattern, pubescence, and cyathial characters conspire to deprive us of any confidence in these speculations. This taxonomically difficult subgenus fairly cries out for careful monographic work but has been successfully avoided by *Euphorbia* specialists and their students for the last 115 years.

One further datum on the species: Dr. Grady L. Webster (personal communication) reports the leaf-anatomy to be typical of plants with non-Kranz photosynthetic pathways. This is to be expected, as all species of *Agaloma* thus far examined are "non-Kranz".

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Point Lobos wildflowers. By Ken Legg. 40 pp., illus. State of California—The Resources Agency, Department of Parks and Recreation. \$0.50. A reissue of the original (1954) publication.

REDISCOVERY OF *BLENNOSPERMA BAKERI* (COMPOSITAE).—An extensive population (ca 120 hectares) of *Blennosperma bakeri* Heiser was discovered recently. The plants were growing with typical vernal pool species in a swale along an intermittent stream: California, Sonoma Co., near intersection of Llano and Todd roads, SW of Santa Rosa, 3 April 1974, *C. F. Quibell 1159* (NCC). This locality is about 27 km WNW of the other two known localities for this rare species. A meiotic chromosome count ($2n = 9 \text{ II}$) agrees with earlier reports of three large and six small bivalents. A few plants (3 of 71) have yellow rather than the typically red style branches in the ray florets.—CHARLES F. QUIBELL, Department of Biological Sciences, Sonoma State College, Rohnert Park, California 94928 and JAMES R. ESTES, Department of Botany and Microbiology, University of Oklahoma, Norman 73069.

TAXONOMIC AND CYTOLOGICAL NOTES ON FERNS FROM CALIFORNIA AND ARIZONA.—*Adiantum jordanii* K. Mull. $2n = 30 \text{ II}$. California: Mariposa Co., 3.5 km (2.2 mi) n of J16 on State Hwy 49, *Smith 644* (UC). This number was predicted by Wagner (Madroño 16:158–161. 1962) on the basis of a count from *Adiantum jordanii* \times *pedatum*.

Bommeria hispida (Mett.) Underw. $2n = 30 \text{ II}$. Arizona: Pima Co., Molina Basin, *MacNeill s.n.* (UC). First chromosome report for the genus.

Cheilanthes cooperae D. C. Eaton. $2n = 30 \text{ II}$. California: Tulare Co., 6.1 km (3.8 mi) E of Kaweah River bridge on State Hwy 198, *Smith 633* (UC); Mariposa Co., State Hwy 49, 2.4 km (1.5 mi) N of jct. with J16, *Smith 643* (UC); Calaveras Co., 5.3 km (3.3 mi) N of Parrots Ferry Bridge, *Smith 647* (UC). First counts for the species. All three populations were found growing on either calcite or dolomite.

Cheilanthes covillei Maxon. $2n = 30 \text{ II}$; 64 spores per sporangium. California: Kern Co., ca 3 km (2 mi) E of Democrat Springs, *Smith 620* (UC). First count for the species.

Cheilanthes intertexta (Maxon) Maxon. I agree with Howell (Amer. Fern J. 50:15–25. 1960) that this species is distinct from *C. covillei* Maxon. The two are sympatric over most of their ranges, although *C. intertexta* is certainly more common northward. In both gross and microscopic characters, *C. intertexta* serves as a

link to *C. gracillima* D. C. Eaton and appears to hybridize with that species. I have seen two collections, both from California, Tuolumne Co., that show morphological intermediacy and have strongly malformed, presumably nonviable spores: Dardanelle, *Alexander & Kellogg 3740* (UC); *Chesnut & Drew s.n.* (UC). These specimens were determined by Carlotta Hall as *Cheilanthes gracillima* var. *aberrans* M. E. Jones, the type of which I have been unable to locate at either POM or US. Cytological verification of this putative hybrid is desirable.

Cheilanthes \times *parishii* Davenp. (pro sp.) It has long been puzzling why this fern has remained so rare and elusive. Howell (Amer. Fern J. 50:15-25. 1960) recorded it only from the type locality (California, Riverside Co., Andreas Canyon). It has since been collected in San Bernardino Co. by Kiefer (Pray, Amer. Fern J. 57:52-58. 1967) and in San Diego Co., Sentenac Canyon, by Witham (H. Witham, *Ferns of San Diego County*, 1972), Kiefer (Pray, loc. cit.), and MacNeill (UC 1398148). Living plants brought back by MacNeill yielded a chromosome count of $2n = 60$ I, and the spores were abortive. The parents of his hybrid are unknown, but the possibilities are few: *Cheilanthes covillei* Maxon and *Notholaena parryi* D. C. Eaton are the most likely candidates, occurring in the same area and occupying similar habitats. The plant in question is more or less intermediate between these two species in dissection and vestiture of the lamina. Only four other cheilantheid ferns occur in San Diego Co. (*C. viscida*, *C. clevelandii*, *Notholaena newberryi*, and *N. californica*) and these only remotely resemble *C. \times parishii*.

Cystopteris fragilis (L.) Bernh. $2n = 84$ II. California: Fresno Co., 1.9 km (1.2 mi) NE of Tollhouse, *Smith 640* (UC).

Notholaena parryi D. C. Eaton. $2n = 30$ II; 64 spores per sporangium. California: Riverside Co., Joshua Tree National Monument, Palm Canyon, *Smith 576* (UC).

Notholaena sinuata (Lag. ex Swartz) Kaulf. var. *sinuata*. $2n = 87$ II. Arizona: Pima Co., Molina Basin, *MacNeill s.n.* (UC). A previous root tip count for this taxon (Knobloch et al., Amer. J. Bot. 60:92-95. 1973) showed $2n = 87$, indicating an apogamous life cycle.

Notholaena standleyi Maxon. $2n = 30$ II; 32 spores per sporangium, from 8 spore mother cells. Arizona: Pima Co., Molina Basin, *MacNeill s.n.* (UC). First chromosome report for the species. A reduced number of spores per sporangium (32 instead of 64) has been taken by some as presumptive evidence of apogamy (Knobloch, Amer. Fern J. 56:163-167. 1966). This is apparently not always the case, since, in this example, eight $2n$ spore mother cells were produced, whereas eight $4n$ spore mother cells are produced in the meiotic obligate apogamous life cycle (Evans, Science 143:261-263. 1964).

Pellaea andromedifolia (Kaulf.) Fée. $2n = 29$ II. California: Tulare Co., 6.6 km (4.1 mi) E of Springville, *Smith 625* (UC); Tulare Co., 9.8 km (6.1 mi) E of Kaweah River bridge on State Hwy 198, *Smith 630* (UC).

Pityrogramma pallida (Weath.) Alt & Grant. $2n = 30$ II. California: Kern Co., 5.0 km (3.1 mi) E of Onyx, *Smith 622* (UC); Tulare Co., 9.8 km (6.1 mi) E of Kaweah River bridge on State Hwy 198, *Smith 631* (UC); Fresno Co., 2.9 km (1.8 mi) NE of Tollhouse, *Smith 641* (UC); Calaveras Co., 0.8 km (0.5 mi) N of Parrots Ferry Bridge, on road to Vallecito, *Smith 603* (UC). These counts agree with the previous report by Alt and Grant (Brittonia 12:153-170. 1960). *Pityrogramma pallida* was growing within ten meters of *P. triangularis* in three of the four populations counted, but intermediate plants were not seen. *Pityrogramma pallida* has usually been treated as only a variety of *P. triangularis* (see, e.g., Tryon, Contr. Gray Herb. 189:52-76. 1962), but the two are very distinct in both living and dried conditions. *Pityrogramma pallida* seems to prefer dryer, better-drained sites than does its relative.

Pityrogramma triangularis (Kaulf.) Maxon var. *triangularis*. $2n = 30$ II. California: Kern Co., 5.0 km (3.1 mi) E of Onyx, *Smith 621* (UC); Tulare Co., 6.6 km (4.1 mi) E of Springville, *Smith 626* (UC). Agrees with previous counts from the Sierra Nevada.

Polystichum \times *californicum* (D. C. Eaton) Diels (pro sp.). [The combining authority is wrongly given as Underwood in Munz (*A California flora*, 1959; *Supplement*, 1968) and in many other places.] $2n = ca\ 82$; five cells counted from three plants, showing from $9\ II + 64\ I$ to $23\ II + 34\ I$. Spores abortive but with many large, globose (unreduced?) spores also present. California: Monterey Co., Pfeiffer Big Sur State Park, Pine Ridge trail, *Smith* 562, 563, 564 (UC). Growing with *P. dudleyi* and *P. munitum*. Wagner (Amer. Fern J. 63:99–115. 1973) showed that *P. californicum* is the hybrid between *P. munitum* and *P. dudleyi*, and my observations confirm this. *Polystichum californicum* exists in both a sterile $2x$ form and a fertile $4x$ form, but only $2x$ plants were encountered in my small sample. Wagner does not elaborate on the distribution of the two cytotypes, and this is a point that ought to be pursued.

Polystichum dudleyi Maxon. $2n = 41\ II$. California: Monterey Co., Julia Pfeiffer Burns State Park, *Smith* 552 (UC); Monterey Co., Pfeiffer Big Sur State Park, Pine Ridge trail, *Smith* 559, 560 (UC).

Polystichum munitum (Kaulf.) Presl. $2n = 41\ II$. California: Siskiyou Co., Callahan to Somes Bar, *Smith* 571 (UC); Monterey Co., ca 2 km (1.2 mi) from Alder Creek campground, *Smith* 598 (UC).

Woodsia plummerae Lemmon. $2n = 76\ II$. California: San Bernardino Co., New York Mts., *MacNeill s.n.* (UC). This is both the first chromosome report for this species and the first certain report of the occurrence of *W. plummerae* in California, a previous report from San Diego Co. being questionable due to possible mixing of labels (Munz, *A supplement to a California flora*, 1968). The mountains of the eastern Mojave Desert are the western limit for several other ferns, including *Notholaena sinuata*, *Cheilanthes feei*, *C. wootonii*, and *Pellaea longimucronata* (Pray, loc. cit.).

I thank Don MacNeill for allowing access to his collection of living ferns, from which several chromosome counts were made.—ALAN R. SMITH, Department of Botany–Herbarium, University of California, Berkeley 94720.

SEED DISPERSAL OF DENDROMECON BY THE SEED PREDATOR POGONOMYRMEX.—Harvester ants, certain Myrmicinae including *Pogonomyrmex*, are such effective seed predators that seed dispersal by ants (myrmecochory) has been considered impossible in the vast hot-arid regions of harvester ant prominence. Berg (Amer. J. Bot. 53:61–73. 1966) demonstrated myrmecochory of *Dendromecon rigida* Benth. in California chaparral but did not document any relationship with harvester ants, either predator avoidance mechanisms or local allopatry. I have found that in early summer *Pogonomyrmex subnitidus* Emery systematically collects seeds of *D. rigida*, removes the elaiosome in the nest, and discards the intact seed. This harvester ant is a dispersal (transport) agent and not a predator of *D. rigida*.

The cooccurrence of the plant and ant were quantified (Sep 1972) on a 27,500 m² site (burned Sep 1970) at Saddle Peak in the Santa Monica Mountains: there were a transect-estimated 200,000 *D. rigida* and 23 *P. subnitidus* nests. The association is enhanced by the failure of *D. rigida* seeds to germinate except after brush fires or severe disturbance, and the requirement of *Pogonomyrmex* for open sites for nesting.

A species of *Campanotus* was also present but its numbers were not estimable. This formicine also transports *D. rigida* seeds, but the discarded seeds remain in subterranean middens. Seeds on *P. subnitidus* middens may readily roll or be washed away. But, while on the midden, they apparently have a significant advantage over uncollected seeds in predation avoidance. In late October a single midden (to 2.5 cm deep, more than 10 m²) contained 522 seeds of *D. rigida*, 464 intact; 23 *Lupinus* seeds were also found, 1 intact. A 3 m diameter sample 15.5 m from the nest and among dense *D. rigida* contained no whole seeds but 23 fragmented seeds; no *Lupinus* were found.

Another case of seed dispersal by harvester ants was subsequently found by Drs. Ruth Bernstein and M. L. Cody of this department in April, 1973, about 25 km south of San Felipe in the Sonoran desert of Baja California. There *Veromessor pergandei* Mayr were transporting appendaged seeds of *Datura discolor* Bernh. to the nest and discarding seeds without appendage from the nest.—STEPHEN H. BULLOCK, Biology Department, University of California, Los Angeles 90024.

REDESCRIPTION OF *ERIOGONUM HOFFMANNII*, A DEATH VALLEY ENDEMIC.—*Eriogonum Hoffmannii* was first collected by Ralph Hoffmann on September 30, 1931, in Wildrose Canyon on the west slope of the Panamint Mountains, Inyo County, California. The species was named and described by Susan G. Stokes (Leaf. W. Bot. 1:23. 1932). Neither the original description nor more recent ones, however, have noted the most distinctive features of the species, particularly characteristics of the calyx lobes in fruit. Apparently this buckwheat is rarely collected and little known.

Having observed it in the field on three occasions, followed by more detailed study of fresh specimens and herbarium material (including an isotype at CAS), I describe it as follows (see also fig. 1):

Annual, 1–5 dm high, glabrous except as noted; stem solitary, or with one or two lesser stems from the base, all with spreading branches; leaves basal, 1–4 cm long, equally wide, suborbicular to subcordate, densely white-tomentose below, less so above; floral bracts minute, ciliate with fine curly hairs; involucre ca 2 mm long, sessile, erect, at the nodes or terminal on short branchlets, many flowered (up to 25), 5-lobed, ciliate with fine curly hairs; calyces 1.5–2.5 mm long, divided to near the base, pale when immature, turning deep pink to wine-red with darker midribs in age; outer segments ovate to lanceolate, tapering from a squarish to slightly cordate base to a narrow blunt tip, thick and rather fleshy with a distinctive vesicular texture; inner segments shorter, thin and translucent, more or less elliptic; achenes pale, slightly longer than the calyx, ca 2 mm long, base broad, tapering to a 3-angled beak of nearly equal length. A common feature of the species is a tuft of short branches stiffly surrounding the lower node, often with lesser tufts at the nodes above and occasionally at the base with the leaves.

Variety *robustus* S. Stokes is a more robust form that grows up to 10 dm high. Besides the sturdy main stem, there are usually several lesser stems. Leaves are 2–5 cm long and 3–8 cm wide, often crisped, and may sheath the base of the stem for 1–3 cm. These larger plants are less inclined to develop the tufts of short branches at the nodes. The inflorescence and achenes are the same.

My field observations were made in the Emigrant Canyon area of the Panamint Mountains, between October 13 and November 13, in the favorable year of 1973. The species was fairly plentiful between 1067 m in the main canyon and 1463 m in a tributary wash. Variety *robustus* was common below, gradually giving way to the type variety as the elevation increased. Variety *robustus* may be merely large specimens of the species growing under more favorable circumstances, such as at lower elevations and where there may be more moisture available. The plants were associated with *Eriogonum brachypodum* T. & G. in the upper range and with *E. Rixfordii* S. Stokes lower in the canyon. *Larrea tridentata* Sesse & Mocino (Creosote Bush) grew on the slopes of the canyon but did not descend to the washes where erigonums grew profusely. *Eriogonum Hoffmannii* matures later than most of its associates and was at its prime in mid-November.

It is probably more than an interesting coincidence that this endemic appears to be restricted to ancient lakebed formations. Perhaps its distribution is determined by an affinity for gypsum or one of its associates. Collection sites for the species are in the Panamint Mountains between 1067 m and 1524 m elevation. Variety *robustus* has also been collected at Furnace Creek Ranch, 366 m, and Ryan Wash, 457 m. Most of these locations are within the boundaries of Death Valley National Monument.—MARY DEDECKER, P.O. Box 506, Independence, California 93526.

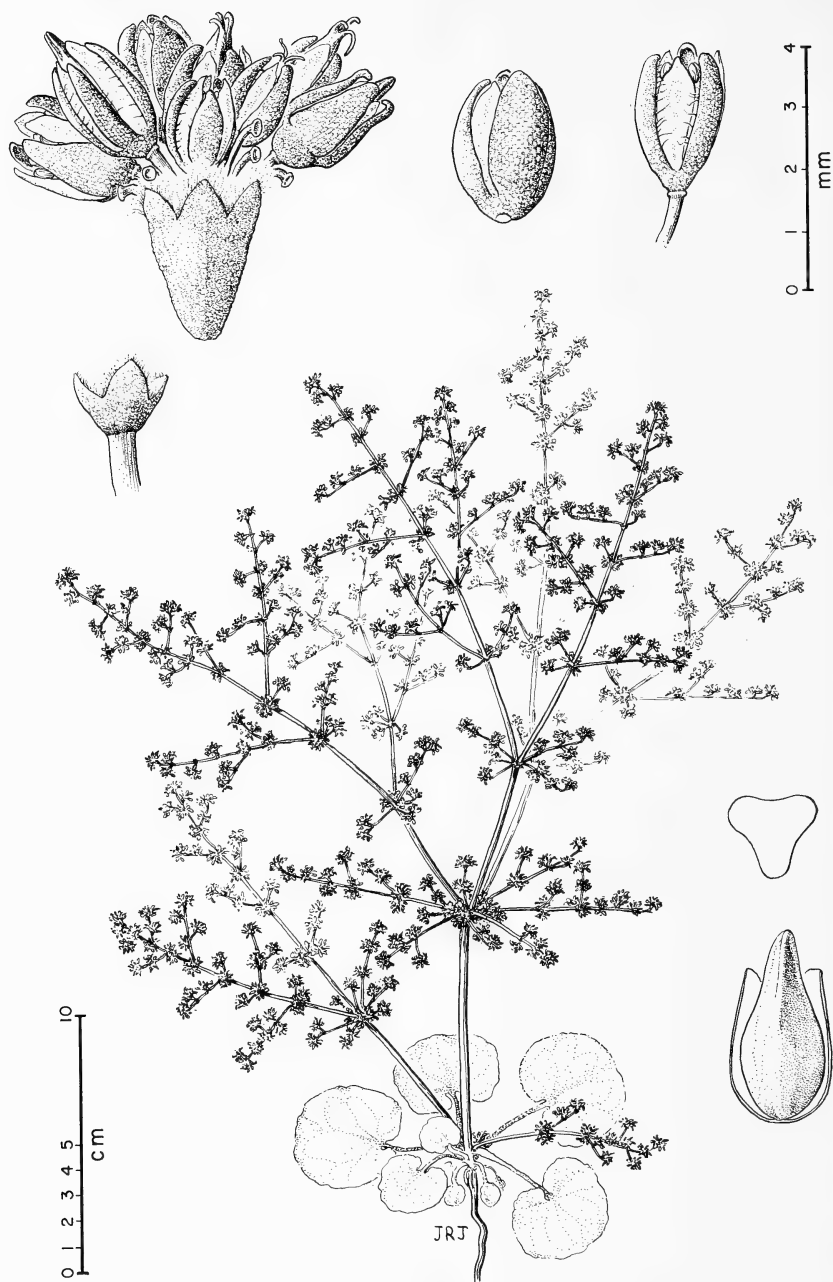


FIG. 1. Habitat and details of *Eriogonum Hoffmannii*. (Based on DeDecker 3365.)



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EFFECTS OF OFF-ROAD MOTORCYCLE ACTIVITY ON MOJAVE DESERT VEGETATION AND SOIL

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In recent years increased use has been made of the desert for off-road vehicle activity, and the resulting disturbance to the landscape has become increasingly noticeable. This study concerns effects of motorcycle disturbance on vegetation and soils of a representative portion of the Mojave Desert. Motorcycle disturbance is here interpreted as the effects not only of motorcycle race trails across the desert but also of off-road parking of vehicles. In fact, the greatest disturbance in a concentrated area apparently takes place in "pit areas", where vehicles are parked at the scene of a race. Intensity of disturbance and size of pit area depend on number and density of vehicles parked, duration of stay, and number of times they return during the year and from year to year. For example, near the study area there is a large pit area (at least 10 ha) from which races have been started for more than ten years. This area is nearly devoid of vegetation, and the soil is hard-packed. Smaller pit areas in the vicinity usually cover one to two hectares, with varying degrees of disturbance to the vegetation and soils, and have been used for racing events only a few times.

Two kinds of motorcycle race take place in this part of the desert—the enduro and the scramble. Both kinds of races follow preset courses or trails that may be as long as 300 km.

The effect of motorcycle disturbance on the vegetation and soil is due to running over plants and disruption and compaction of surface soil. Thus, if disturbed areas were compared to equivalent undisturbed areas, reduction in total numbers of plants, reduction in number of plant species, increase in the number of dead shrubs, and increase in the bulk density or degree of compaction of the soil in disturbed areas would be expected.

Disturbance both to pit areas and to trails was studied. One representative pit area and one trail were used for vegetation and soil analysis, and sample plots and/or transects were established. Adjacent to these disturbed areas, equivalent sites, which were not disturbed by motorcycle activity, were similarly studied.

SITE DESCRIPTION AND METHODS

Pit Area—Site A is located 12–16 km NE of California City, Kern County, California, in low, rolling hills. This pit area had been used several times prior to 1973 but had not been disturbed for the past year. The degree of disturbance was only moderate compared to that of other pit areas in this part of the Mojave Desert. The vegetation at this location and at the trail site described later belongs to the Creosote Bush Scrub community as described by Munz (1959). The soil at Site A and also at the trail site was formed of unconsolidated alluvium derived from the adjacent uplands, which are largely granitic and metamorphosed sedimentary rock. At Site A, the soil is a sandy loam, pH 8.0, lacking CaCO_3 .

A 1 ha plot that covered most of the area of intense disturbance was subjectively established on the Site A pit area. In order to compare the pit area disturbance with equivalent, relatively undisturbed vegetation, a control 1 ha plot was subjectively established several hundred meters away from the pit area. An effort was made to select an equivalent site with respect to potential vegetation, topography, and surface soil.

Within both plots at Site A, two parallel 100 m transects were established, each transect lying 20 m from a side of the hectare plot and oriented perpendicularly to the direction of the slope. Herbaceous plants were sampled along each transect using a 0.25 m² quadrat placed every 4 m along the transects. Numbers of individuals of each species rooted within the quadrat were recorded in each quadrat. Shrubs were sampled by recording the presence of all shrubs rooted within a 3 m wide strip along one side of each transect. For each individual shrub, position along the transect and a visual estimate of the diameter of the canopy were recorded. For statistical analysis it was necessary to divide shrub data taken from each plot into ten equal and consecutive sections, each representing 60 m².

Six randomly selected soil samples were taken from the disturbed plot and five randomly chosen samples were taken from the undisturbed plot. Two methods were used to obtain soil samples. The core method was used for the undisturbed plot, and the clod method was used for the disturbed plot, where the coring instrument could not be driven into the hard, compacted soil. These two methods are described in detail by G. R. Blake (1965).

The average pore space for each sampled area was determined, using the equation:

$$\text{pore space (\%)} = 100 - (D_b/D_p \times 100)$$

where D_b is the bulk density of the soil, and D_p the average particle density, usually about 2.65 g/cc (Hausenbuiller, 1972).

Trail—Site B is a portion of a 240 km trail made by a motorcycle enduro race on 7–8 April 1973. Sampling was done on 14–15 April 1973 on a short length of this trail, about 11 km west of Randsburg, Kern County, California. The landscape is a gently sloping plain intersected with shallow washes. The soil is a fine sandy loam, pH 7.0, lacking CaCO_3 .

A 100 m transect was established along the middle of the trail. A 3 m long rod was placed perpendicularly to the transect every 8 m, and herbaceous plants were sampled using 0.25 m² quadrat placed on one side of the rod within each of the three meters of the rod. The number of individual plants of each herbaceous plant species rooted within the quadrat was recorded. Shrubs were sampled by recording the presence of all shrubs rooted within a 3 m wide strip along the same side of the transect. For each individual shrub, position along the transect, distance from the transect, and diameter of the canopy were recorded.

In order to demonstrate degrees of disturbance related to distance from the center of the 3 m wide trail, the data were compiled as three parallel subtransects: subtransect 1 (center of trail); subtransect 2 (edge of trail); subtransect 3 (off the trail).

The same sampling technique used on the trail was used for a 100 m transect parallel to the trail and about 50 m away. This transect was considered to be in relatively undisturbed vegetation. Data from three subtransects within this control transect were combined.

Thus thirty-nine 0.25 m² quadrats for each 100 m transect were sampled for herbaceous plants, and 300 m² of continuous area was sampled for shrubs. For statistical analysis, it was necessary to divide the shrub data taken from each transect into ten equal and consecutive sections, each representing 30 m².

Five soil samples were taken at 30 m intervals along the disturbed transect in the middle of the trail and also along the undisturbed transect. The core method described earlier was used to obtain the soil samples.

RESULTS

In general, the data are presented in this section so as to compare aspects of vegetation and soils in the disturbed areas to those at the matched undisturbed areas. Pertinent differences in both the vegetation and soils data were tested for their statistical significances, using the one-tailed *t*-test for two independent samples (Siegel, 1956).

Vegetation Data. Numbers and frequency of each species of herbaceous plant are shown for each plot or transect in Tables 1 and 2. Numbers and average canopy cover per individual for each species of shrub in the plot or transect are shown in Tables 3 and 4. The numbers of dead shrubs are included.

TABLE 1. HERBACEOUS VEGETATION AT PIT AREA (SITE A). N = number of individuals encountered. F = frequency of encounter in total of fifty 0.25 m² quadrats.

	Disturbed plot		Undisturbed plot	
	N	F	N	F
<i>Astragalus didymocarpus</i>	13	0.10	33	0.28
<i>Amsinckia intermedia</i>	18	0.10	13	0.14
<i>Baeria debilis</i>	19	0.12	695	0.78
<i>Chaenactis fremontii</i>	24	0.28	35	0.36
<i>Chorizanthe brevicornu</i>	2	0.04	2	0.04
<i>Coreopsis calliopsidea</i>	1	0.02
<i>Cryptantha micrantha</i>	1	0.02	1	0.02
<i>Cryptantha nevadensis</i>	1	0.02
<i>Eriogonum gracillimum</i>	3	0.06
<i>Eriogonum pusillum</i>	1	0.02
<i>Eriophyllum pringlei</i>	19	0.08
<i>Erodium cicutarium</i>	601	0.88	1043	1.00
<i>Eschscholzia minutiflora</i>	16	0.12	11	0.16
<i>Filago depressa</i>	1	0.02
<i>Gilia minor</i>	9	0.10	54	0.40
<i>Lepidium flavum</i>	55	0.22
<i>Lotus strigosus</i>	21	0.22
<i>Malacothrix coulteri</i>	8	0.16
<i>Malacothrix glabrata</i>	2	0.02
<i>Mentzelia veatchiana</i>	9	0.10	14	0.14
<i>Nama demissum</i>	10	0.14
<i>Pectocarya platycarpa</i>	1	0.02
<i>Phacelia fremontii</i>	3	0.04	12	0.16
<i>Phacelia tanacetifolia</i>	1	0.02	2	0.04
<i>Plagiobothrys arizonicus</i>	10	0.12
<i>Schismus barbatus</i>	191	0.72	38	0.14
<i>Syntrichopappus fremontii</i>	1	0.02
<i>Thelypodium integrifolium</i>	30	0.46	1	0.02
Totals	980		3615	

According to the hypotheses stated in the introduction, motorcycle disturbance was expected to cause a decrease in the number of live plants, an increase in the number of dead shrubs, a decrease in the average canopy per individual shrub, and a decrease in diversity in an area where disturbance had occurred. In nearly all cases, the data show increases or decreases where they are expected. In a few instances the expected trends are reversed: number and cover per shrub of *Acamptopappus sphaerocephalus* in both sites; number of dead shrubs in Site A; canopy cover per shrub of *Ambrosia dumosa* in Site B; and number of *Schismus barbatus* in Site A. In regard to plant diversity, an obvious decrease in the number of species is seen in the herbaceous vegetation at Site B. Fourteen species were counted in the undisturbed transect, but only seven species were counted in the disturbed transect.

TABLE 2. HERBACEOUS VEGETATION AT TRAIL (SITE B). N = number of individuals encountered. F = frequency of encounter in total of thirty-nine 0.25 m² quadrats.

	Disturbed plot					Undisturbed plot	
	N				F	N	F
	(subtransects)						
	1	2	3	Σ			
<i>Amsinckia intermedia</i>						1	0.03
<i>Anisocoma acaulis</i>	1	0	2	3	0.08	1	0.03
<i>Cryptantha micrantha</i>	0	1	2	3	0.08	2	0.03
<i>Cryptantha pterocarya</i>	0	2	0	2	0.05	2	0.03
<i>Erodium cicutarium</i>	0	0	5	5	0.08	12	0.12
<i>Gilia latifolia</i>						3	0.03
<i>Lupinus odoratus</i>						1	0.03
<i>Malacothrix glabrata</i>						3	0.08
<i>Malvastrum exile</i>	0	1	6	7	0.05	4	0.03
<i>Mentzelia veatchiana</i>	3	10	6	19	0.26	45	0.54
<i>Nama demissum</i>						1	0.03
<i>Oenothera dentata</i>						3	0.05
<i>Plagiobothrys arizonicus</i>						1	0.03
<i>Schismus barbatus</i>	4	48	48	100	0.61	315	0.95
Totals	8	62	69	139		394	

Statistical tests comparing differences between disturbed and undisturbed areas at each site gave confidence points equal to or less than 0.2 to the following values: total numbers of herbaceous plants at both sites (0.001); total numbers of *Ambrosia dumosa* shrubs at Sites A and B (0.2 and 0.05, respectively); average canopy cover per *Ambrosia dumosa* shrub at Sites A and B (0.01 and 0.2, respectively); and average canopy cover per *Larrea divaricata* shrub at Site A (0.1).

Soil Data. In Site A, the disturbed plot soil had an average bulk density of 1.67, with an average pore space of 37.0 percent, and the undisturbed plot had an average bulk density of 1.46 with an average pore space of 45.0 percent. The confidence point of the difference between these average bulk densities is 0.005. In Site B, the disturbed transect (trail center) had an average bulk density of 1.66, with an average pore space of 37.3 percent. The undisturbed transect had an average bulk density of 1.59, with an average pore space of 40.0 percent. The confidence point of the difference between these average bulk densities is 0.1.

It is possible that the clod method, used for the disturbed plot of Site A, gave higher values for the bulk density than the core method would have given, since the clod method did not take interclod spaces into account. However, it was noted at the time the samples were taken that few interclod spaces or cracks existed in the disturbed plot soil at Site A.

TABLE 3. SHRUB VEGETATION AT PIT AREA (SITE A). D = disturbed plot. U = undisturbed plot. Number = numbers of living shrubs encountered. Cover = average canopy cover per shrub (m²).

Taxon	Number		Cover	
	D	U	D	U
<i>Acamptopappus sphaerocephalus</i>	22	2	0.06	0.04
<i>Ambrosia dumosa</i>	25	52	0.06	0.14
<i>Eurotia lanata</i>	1	0.02
<i>Larrea divaricata</i>	26	28	0.95	1.33
<i>Lycium andersonii</i>	1	0.20
<i>Machaeranthera tortifolia</i>	1	0.02
<i>Tetradymia stenolepis</i>	6	0.48
Total living shrubs	75	89		
(Dead shrubs	74	52)		

DISCUSSION AND CONCLUSIONS

Vegetation. Statistical treatment of the data points out only one consistently significant difference between disturbed vegetation and undisturbed vegetation—namely, a loss of the herbaceous plant cover in both sites. Even more indicative of this effect are the totals of herbaceous plants on the three subtransects of the disturbed transect on Site B, which show a drastic decline in the number of herbaceous plants in subtransect 1, the middle of the motorcycle race trail (See Table 2). The relative permanence of the loss of the herbaceous vegetation is shown in the data from Site A, which was not disturbed during the 1973 growing season. At this site herbaceous plants had not returned to their normal densities.

Two introduced species, *Erodium cicutarium* and *Schismus barbatus*, are the most common herbaceous species found on the study sites. At Site A, *Schismus barbatus*, an annual grass, is the only herbaceous species for which densities were higher in the disturbed areas than in the undisturbed. At Site B, disturbance occurred only one week prior to sampling, and many *Schismus barbatus* plants present along the trail were destroyed at that time. Evidently, density of *Schismus barbatus* increased following disturbance at Site A; it is reasonable to expect that the numbers of this species will also greatly increase along the trail at Site B in the next growing season.

Based on statistical analyses, definitive conclusions cannot be made on the effects of motorcycle activity on the vegetation other than the significant loss of herbaceous vegetation. Nevertheless, with few exceptions, the data show an overall trend toward fewer plants and less cover per individual shrub in the disturbed areas than in undisturbed areas.

TABLE 4. SHRUB VEGETATION AT TRAIL (SITE B). D = disturbed plot. U = undisturbed plot. Number = numbers of individuals of living shrubs encountered. Cover = average canopy cover per shrub (m^2).

Taxon	Number				Cover	
	D				U	
	(subtransects)				D	U
	1	2	3	Σ		
<i>Acamptopappus</i>						
<i>sphaerocephalus</i>	8	20	16	44	29	0.12
<i>Ambrosia dumosa</i>	12	45	24	81	135	0.22
<i>Eurotia lanata</i>	3	0.17
<i>Larrea divaricata</i>	1	7	7	15	13	0.51
Total living shrubs	21	72	47	140	180	
(Dead shrubs	14	27	24	65	51)	

It is believed that the ambivalent results of the statistical tests reflect subtle site differences between disturbed and undisturbed plots and transects, not the lack of effect from motorcycle disturbance. The effect of site differences on the data might have been lessened by more extensive sampling. Evidence for possible non-equivalence of disturbed and undisturbed plots is: (1) a greater number of shrubs in disturbed plots than in undisturbed plots (*Acamptopappus*, Sites A and B; *Larrea*, Site B); and (2) greater cover per individual plant in disturbed plots than in undisturbed plots (*Acamptopappus*, Sites A and B). These differences in the vegetation could be due to variation of such factors in the soil as depth, composition, or moisture. If such variations caused an increase in the density and cover of shrubs in the disturbed plots or transects, the effects of motorcycle disturbance would be masked.

Significance of the data for dead shrubs is not known because of the difficulty of reliably determining whether a plant was destroyed by a motorcycle or whether it died naturally and had disintegrated. The situation in Site A where more dead shrubs were found in the undisturbed plot than in the disturbed plot may be explained as follows: The Site A pit area has been used a number of times in the past several years, but not during the present year. Many dead shrubs on the disturbed plot may have disintegrated and blown away or have been used as firewood by cyclist groups, resulting in fewer dead plants as compared to the undisturbed plot.

At Site B, the paucity of shrubs in disturbed subtransect 1 (trail center) would seem to reflect a significant destruction of shrubs by motorcycles. While this is undoubtedly true to some extent (reflected by the significantly smaller total number of shrubs in the disturbed transect compared to the undisturbed transect), caution is used in mak-

ing this interpretation. When numbers of shrubs in subtransects 2 and 3 of the disturbed transect are compared, the number of shrubs in subtransect 3 was found to be less (Table 4). This was not expected, since subtransect 2 was closer to the center of the trail. Further, canopy cover per individual *Ambrosia dumosa* shrub in subtransect 3 exceeded that in subtransect 2. The probability of either of these differences occurring by chance is 0.1. These observations indicate the existence of some pattern in the vegetation bordering the trail. In reality, it is reasonable to assume that the first cyclists to run the race did not ride in a straight line oblivious to the shrubs, but rather, guided their vehicles between the shrubs. Most shrubs that were avoided by the cyclists were recorded in subtransect 2, resulting in the high number of shrubs in that subtransect. Whether the cyclists made their own pattern through the vegetation or whether they were inadvertently following some natural pattern in the shrub vegetation is not known. In either case, if the trail were widened by increased use, the large number of shrubs bordering the trail would be damaged or destroyed.

Soils. Pore space of a soil is the volume that is not taken up by solid particles; it normally contains air and water. This space consists of macropores that allow the ready movement of air and water, and micropores in which air movement is impeded and water moves largely by slow capillary movement. Desert soils of this area are relatively coarse, with a relatively high proportion of larger particles such as sand and gravel. Sandy soils normally show a range of 35 to 50 percent pore space, while heavy surface soils with a larger clay content show a range of 40 to 60 percent pore space (Buckman and Brady, 1960).

With greater compaction from off-road vehicles, soil particles are pressed closer together and the bulk density is increased. The small increase in bulk density seems insignificant when the disturbed areas are compared to the undisturbed; there is probably a proportionately larger decrease in the percentage of macropores in the disturbed areas.

The increase in bulk density of disturbed soils as shown in this study, with the resulting decrease in macropore space, probably decreases the amount of water that the soil can hold and the rate at which water can flow through the soil (Yang and DeJong, 1971). It also reduces the permeability of the soil so that runoff is greater (Kubota and Williams, 1967). Consequently, there is a reduction of the water stored in the soil and available for plant growth.

Since the storms in the Mojave Desert are generally short and intense, much of the rainfall cannot be absorbed by the soil and runs off the surface (Troxell and Hoffman, 1954). Desert rainfall is also very low and sporadic in the Mojave Desert: 50–130 mm per year, with occasional completely dry years and others with as much as 230 mm (K. Berry, personal communication). Because of this climate factor, and

because the sandy desert soils are never high in available water, lack of soil water is a limiting factor, and any decrease in the amount of water entering the soil and available for plants would certainly be detrimental to the vegetation in a disturbed area.

In addition to possible decrease of available water in the soil due to compaction, there may be a more direct effect on plants. Kubota and Williams (1967) found that compaction of a light sandy loam decreased germination, root growth, and size of shoots of barley and globe beet. Phillips and Kirkham (1962) showed that compacted soils impeded root growth. The somewhat unimpressive differences in bulk density of the sampled soils belie the actual hardness of the compacted soil in the disturbed areas compared to that of undisturbed desert soil. While a sharpened metal stake could usually be shoved by hand into the undisturbed soil, it required a sledge in most locations of both the pit area and the trail. It seems likely that this hardness of the soil of disturbed areas would inhibit the growth of roots of desert plants that are adapted to a looser soil condition.

There is evidence that the effects of either lack of soil water or root growth impedance, or both, may be influencing vegetation at Site A. Although the Site A pit area was not disturbed during the 1973 growing season, density of annual plants was very low compared to adjacent undisturbed areas. Since the supply of light-weight seeds from annual plants growing in surrounding areas is probably more than sufficient to reseed the pit area, it appears that the compacted soil in the Site A pit area is no longer an adequate seedbed for seed germination and seedling growth.

ACKNOWLEDGMENTS

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A NEW SPECIES OF HACKELIA (BORAGINACEAE) FROM OREGON

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During the preparation of a revision of some of the northwestern American taxa of *Hackelia*, specimens representing an undescribed species were encountered. The taxon is known only from the Three Forks region of the Owyhee River, southeastern Malheur County, Oregon. It was apparently first collected by Milton L. Dean, who did a floristic study of the area in 1957 and 1958 (Dean, 1960).

Hackelia ophiobia R. L. Carr, sp. nov.

Planta perennis viridis, radice crassiuscula gradatim angustata, caudicibus fasciculatis ab petiolis persistentibus vestitis. Caules graciles sparsim strigosi. Folia rosulae longiuscule petiolata, ovata vel oblonga, 5-15 cm cum petiolo longa, 15-35 mm lata, apice obtusa mucronulata, basi nunc truncata nunc cordata, aequabiliter hirsutula. Folia caulium elliptica vix reducta, inferiora in petiolum attenuata, superiora sessilia, omnia hirsutula. Inflorescentia laxa ramosa, bracteis inferioribus usque 2 cm longis, superioribus gradatim parvioribus. Pedicelli recurvi 12-17 mm longi. Lobi calycis strigillosi lanceolati acuti 3-4 mm longi. Corolla limbo rotato 6-8 mm lato caeruleo, tubo albido vel flavo calyce aequilongo. Fornices corollae truncato-rotundati breviter papillati. Nuculae ovoideae, 2.3-3.3 mm longae 1.2-2.1 mm latae, dorsaliter parum glochidiatae, muriculatae, vix alatae, aculeis marginalibus principalibus 1.0-1.5 mm longis, ad basim distinctis, cum aculeis brevioribus interspersis. Cicatrix nuculae ad centrum, ovata. Figures 1 and 2.

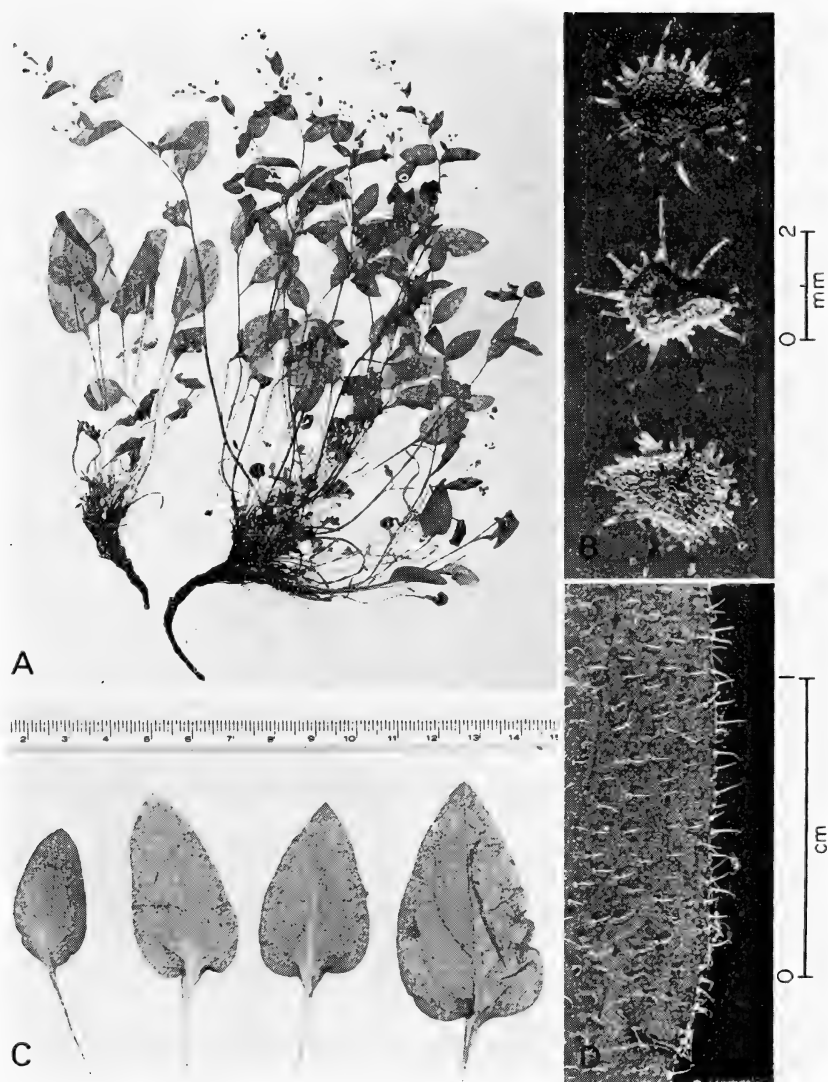


FIG. 1. *Hackelia ophiobia*. A, habit; B, basal leaves; C, nutlets; D, leaf pubescence.

TYPE: Oregon, Malheur Co., Owyhee River canyon at Three Forks, 30 June 1968, R. L. Carr 433 (Holotype: OSC; isotypes: NY, WS, US, GH).

ADDITIONAL SPECIMENS EXAMINED: Carr 514 (NY, WS, US, GH, OSC), Dean 116 (A, OSC), Dean 246 (OSC), Dean 281 (OSC).

HABITAT: In mostly well-shaded, sandy talus in cracks and crevices of rocky basaltic bluffs and cliffs.

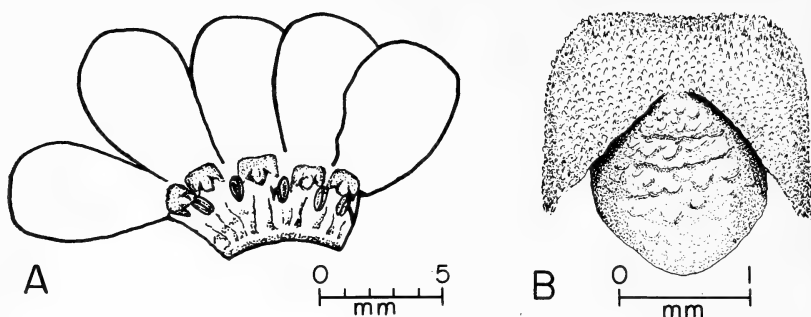


FIG. 2. *Hackelia ophiobia*. A, corolla; B, corolla appendage with protuberance.

The basal leaves of *Hackelia ophiobia* (fig. 1,B) are unique among species of *Hackelia* endemic to western North America in having a broad, short, truncate to cordate blade and a long slender petiole. The stems are very slender, the herbage is thin and bright green, and the inflorescence is very lax and sparsely flowered. Morphologically the flowers and nutlets of *H. ophiobia* approach those of *H. cusickii* (Piper) Brand. The nutlets (fig. 1,C) differ in being smaller and in commonly having fewer glochidia on the dorsal surface. The corolla is smaller and differs in having a short, deltoid protuberance on the very short-papillate fornicies (fig. 2,B). Fornices of *H. cusickii* are more distinctly papillate and have a longer, often pandurate protuberance.

The habitat of *Hackelia ophiobia* is sharply limited. The plants grow near the bases of cliffs or large outcroppings of basalt in areas where there is little if any competition from other vascular plants. As a diploid ($2n = 24$) it differs sharply from other known diploids such as *H. micrantha* (Eastwood) J. L. Gentry, *H. floribunda* (Lehm.) Johnst., *H. amethystina* J. T. Howell, *H. bella* (Macbr.) Johnst., and *H. californica* (Gray) Johnst., which are very robust plants. It is likely that these taxa represent a group of related diploids phylogenetically quite distinct from *H. ophiobia*.

Although presently known only from the Three Forks region, *H. ophiobia* quite probably will be found at other sites in the Owyhee River canyon. Its habitat appears to be well represented along the Owyhee River and in the Bruneau River canyon, which is the next watershed to the east. This region of remote and inaccessible deep canyons has been very poorly botanized and this quite probably accounts for the late discovery of this unique *Hackelia* species.

The Latin description was prepared with the assistance of Kenton L. Chambers.

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CARL BRANDT WOLF, 1905–1974

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Carl Brandt Wolf was born to George Henry Wolf and Emma Amelia (Brandt) Wolf in Freesoil, Michigan, on March 22, 1905. The family moved to Oregon in 1910 and lived in or near Medford until June, 1915. They went to San Diego, California, at that time, and thence to Eagle Rock on the outskirts of Los Angeles a year later. Here Carl completed grammar school, graduated from Glendale High School in 1921, and entered Occidental College in September at the age of sixteen. At the end of his first year in college he decided he wanted some work-a-day experience and a bit more maturity before continuing his college training, so took a job with the Theodore Payne Nursery in Los Angeles. He maintained a close friendship with Mr. Payne throughout the remainder of Payne's life, and for a number of years served as a member of the Advisory Board of the Theodore Payne Foundation, a non-profit foundation dedicated to preservation of California's native trees, shrubs, and perennial wildflowers and to promotion of their use in ornamental plantings.

Following the year with Payne Nursery, Carl returned to college at Occidental, receiving his A.B. with a major in botany in 1926. He immediately began graduate work at Stanford University under the guidance of Dr. LeRoy Abrams, and qualified for a Master's degree in June, 1927. He pushed right ahead toward the Ph.D., continuing his study of native California plants, concentrating on the taxonomy and distribution of *Rhamnus*. In addition to his own classroom studies, Carl accepted a Teaching Assistantship, an appointment he held almost continuously until completion of work for the Ph.D., in 1930. Concurrently with meeting classes and laboratory sections, he did an amazing amount of field work, for he spent many weekends and nearly every available holiday pursuing his field observations and collecting high quality herbarium specimens. His field operations extended from the Canadian to the Mexican borders, and east into Nevada, Arizona, and New Mexico. His field notes were meticulous and voluminous, and labels accompanying his herbarium specimens bore much more than the usual amount of information supplied by contemporary botanists.

Carl was elected to The Society of the Sigma Xi in the spring of 1930. On June 14th he married Dorothy Anne Rhodes whom he had met at Occidental College in 1925. In September he accepted an appointment as Botanist at Rancho Santa Ana Botanic Garden, then located in lower Santa Ana Canyon in Orange County, California. He held that position until 1945.



Carl Brandt Wolf, April, 1964.

During that decade and a half, he carried on extensive field work, collecting thousand of herbarium specimens and hundreds of propagules to be moved into the Garden's experimental plots. He travelled widely to make these collections and once estimated that in criss-crossing California he had been within 25 miles or less of every point within the state!

Among native plants selected for ornamental testing was a strain of *Platanus racemosa* that grew rapidly during its early stages, often at-

taining a height of two to three meters in four or five years. He gave attention to many other native plants, among which were species of *Cupressus*, *Pinus*, *Arctostaphylos*, *Ceanothus*, *Eschscholzia*, *Fremontodendron*, *Garrya*, *Quercus*, *Ribes*, *Romneya*, and many others.

While living in Fullerton (a few miles from the Rancho Santa Ana Botanic Garden), Carl began to set a pattern of civic service that characterized the rest of his life. He was elected to the Board of Trustees of the Fullerton High School and Junior College in 1942, and served until midyear, 1945, filling the President's chair during 1944-45. He was active in the Masonic Lodge and became a Shriner after moving to Fillmore.

In 1945 Carl resigned as Botanist at Rancho Santa Ana Botanic Garden to become manager of the Sespe Land and Water Company and of McNab Estate Company, both of which, as well as the town of Fillmore, had been founded by his wife's grandfather, J. D. McNab, in 1886. Carl retained the managerial position until holdings of both companies were sold in 1967. During the 22 years he managed the family holdings, Carl devoted little time to experimental botany. He did, however, carry forward selection of citrus rootstock and development of productive strains of avocado trees. Also, he started and operated La Cienega Nursery, which specialized in citrus and avocado stocks. He experimented with several strains of ornamental citrus plants and considered the "Chinotto" one of his most successful developments. It is a dwarf tree that produces abundant crops of golden fruit that, although inedible, hang on the tree for six to eight months, enhancing its ornamental value.

Health problems beset Carl intermittently from 1960, when a kidney ailment nearly cost him his life, until his death on February 10, 1974, a little more than a month before his 69th birthday. Throughout that trying period he retained an optimistic outlook. He kept a keen interest in plants and their uses, in the history of his home area, and in the welfare of his fellow men. All those who knew him lament his passing. May his memory live long among his associates and friends.

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- NOTE: A number of popular articles by C. B. Wolf were published in the *Fillmore Herald*.

MALACOTHRIX TORREYI (COMPOSITAE), A NEW RECORD FROM CALIFORNIA.—In a recent note (Madroño 21:535. 1972), Hardham and True discuss evidence concerning the occurrence of *Malacothrix torreyi* Gray in California and conclude that the only unequivocal collection of that species in the state is from Mono County (*Hardham 15084*, CAS). To this record I now add my collections from Inyo County, California, along U.S. 190 near the junction with the road to Darwin (*Davis 21-57, 22-57, 27-57, 30-58, 31-58, and 32-58*, DHL). I found these populations while visiting a locality described on the label of an herbarium specimen of *M. sonchoides* T. & G. *Malacothrix sonchoides* has been considered by some to be conspecific with *M. torreyi* (Williams, Amer. Midl. Naturalist 58:494-512. 1957), and is sometimes identified as the latter species by collectors not familiar with *Malacothrix*. The distribution of *M. sonchoides* and *M. torreyi* along U.S. 190, as observed in 1957 and 1958, was correlated with elevation. Pure populations of *M. sonchoides* occurred at 1280-1340 m, a mixed population of *M. sonchoides* and *M. torreyi* was found at 1417 m, and pure populations of *M. torreyi* occurred at 1463-1585 m. No evidence of hybridization was found in the mixed population and plants of the two species were easily distinguishable on the basis of vegetative differences and differences in flower color.

In the course of preparing a monograph of *Malacothrix*, I have looked at numerous collections of *M. torreyi* from many herbaria and have plotted its distribution in Arizona, California, Colorado, Idaho, Nevada, Oregon, Utah, and Wyoming. From these plots it appears that the populations of *M. torreyi* in Inyo County, California, are relictual.—W. S. DAVIS, Department of Biology, University of Louisville, Kentucky 40208.

H. LESCHKE, H. M. POLLARD, L. S. ROSE, AND
E. C. TWISSELMANN: OBITUARIES

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During the past two years the Department of Botany of the California Academy of Sciences lost four Research Associates. The following accounts briefly characterize their backgrounds and contributions to botany.

Hans Leschke (1883–1973), a native of Germany, came to San Francisco in 1924 as director of the newly created Municipal Chorus. Alfred Hertz, conductor of the San Francisco Symphony Orchestra, invited Dr. Leschke to direct the chorus for a spring festival in San Francisco. The festival was so great a success that it was decided to establish for San Francisco a permanent municipal chorus with Dr. Leschke as director. At his retirement from that directorship in 1964, he received several awards and citations for his successful achievements in music.

In addition to his life-long interest in music Dr. Leschke had another interest, which was in natural history and botany. From the University of Berlin he received a doctorate in paleontology. But apparently he had a greater interest in plants than fossil animals for during all of his years in San Francisco his spare time away from music was devoted to hiking and studying plants along the way. In the late 1930's he met John Thomas Howell through Sierra Club activities and this led to his association with the Academy.

During a number of summers Dr. Leschke and his wife spent vacations and camping trips in Lassen Volcanic National Park. Intensive field work during these summers resulted in his later collaboration with George W. Gillett and John Thomas Howell in *A Flora of Lassen Volcanic National Park, California* published in 1961.

In addition to his field studies in Lassen Park, Dr. Leschke also collected extensively in Olympic and Mt. Rainier national parks in Washington. His local interest centered in Marin County and Mt. Tamalpais in particular, where his field work was of great help to Mr. Howell when he was preparing his *Marin Flora*.

Dr. Leschke had a broad knowledge of western plants but he developed a particular and critical interest in the large difficult genus *Carex*. The Academy Herbarium has an exceptionally fine collection of this genus and Dr. Leschke spent much time during his later years critically working on this material.

On his field trips Dr. Leschke always collected specimens, which he brought to the Academy Herbarium for identification. He deposited a

set of his collections there but in addition he kept a small personal herbarium, which on his death was presented to San Francisco State University.

A rare Indian paint-brush known only from Point Reyes Peninsula in Marin County, *Castilleja Leschkeana*, was named by Mr. Howell in honor of Hans Leschke.

Henry Minter Pollard (1886–1973), born in Mendota, Illinois, and a graduate of Mendota (now Aurora) College, had a long career as a teacher of Latin and Greek. He came to California in the early 1900's and taught classical languages in Marin County, Catalina Island, the Ojai Valley in Ventura County, and the Santa Barbara area, always in private schools.

During summer vacations Mr. Pollard enjoyed such out-of-door activities as hunting and fishing and he always observed the natural features, geology, plants, birds and mammals, of the areas he visited. Orleans in Humboldt County was one of his favorite fishing places during his years of teaching in Marin County. It was while teaching in Marin County that he became acquainted with John Thomas Howell and the Academy. He occasionally brought plant specimens to the Academy Herbarium for identification. He had no formal training in botany but his interest in plants led him to study their intricacies by himself and Mr. Howell pointed out to him the value of making collections.

While teaching in the Ojai Valley in the 1940's, Mr. Pollard began extensive collecting of the Ventura River drainage basin. It was in this area during the 1950's and 1960's that he saw the many changes brought by industry and development. These changes destroyed much of the native flora and allowed many non-native introduced weeds to become established. Later, in Santa Barbara, he saw the city grow as small, undeveloped areas within the city limits were converted to residences and shopping centers. His only published paper was a list of native plants collected in such a small area in Santa Barbara before the plants disappeared in the path of urbanization (Wasmann J. Biol. 17:153–156).

As these developments took place he noted that the native plants were replaced by agricultural and urban weeds. His approach to these replacement plants was not to ignore their presence but to collect them. This resulted in many first, or at least early, records of the appearance of new weeds for Ventura and Santa Barbara counties. Such information has been valuable and useful to the California Department of Food and Agriculture in its survey of the weeds of the State.

Mr. Pollard made his collections by walking. Although in his early years he drove a Model T Ford, during his collecting years he did not own an automobile and he often referred to automobiles as necessary evils of modern times. Since he liked both walking and collecting, he recollected many of the same plants in the same areas. His early col-

lections came to the Academy Herbarium. The specimens, usually in duplicate sets, were used not only for deposit there but also provided much useful material for exchange with other herbaria. In addition to the Academy Herbarium, his major collections are at the Santa Barbara Botanic Garden (especially collections of the 1960's and early 1970's), Santa Barbara Museum of Natural History, and Rancho Santa Ana Botanic Garden.

Lewis Samuel Rose (1893-1973), a native San Franciscan, was associated with the Academy for more than forty years. As a student at the University of California, Berkeley, he was interested both in botany and entomology but he finally chose botany. At that time he considered specializing in algae through encouragement from William A. Setchell. After graduation in 1917, he spent a year in Japan making collections that he later presented to the University. The algae and his other early collections were made under the name L. S. Rosenbaum, his original family name. Following a short army career during World War I and several years as an account executive, he became a volunteer worker in the Academy's Department of Botany in 1930.

During subsequent years he spent much of his time and effort collecting plants in large sets. These he used in an exchange program. During the 1930's he sought and built up a number of exchanges with various individuals and institutions in different parts of the world, including Europe, eastern Asia, South Africa, Australia, and Argentina. Mr. Rose carried on this kind of collecting and exchanging throughout the remainder of his life. Not only did he send thousands of specimens of California plants to herbaria around the world, but in return he received a commensurate amount of material, which he donated to the Academy. It has been estimated that through his collection and exchange activities this herbarium received about 100,000 specimens.

For many years Mr. Rose maintained in the Academy Herbarium an index file for all of those plants having their type localities in California and other western states. He kept the file up to date by searching through current literature, particularly monographs and revisions, where new species were described.

Through the years Lewis Rose's many collections turned up interesting material including a number of new species, ten of which were named for him. These include *Castilleja Roseana* Eastwood, *Arctostaphylos Rosei* Eastwood, *Arenaria Rosei* Maguire & Barneby, and *Senecio Lewisrosei* J. T. Howell.

Ernest Christian Twisselmann (1917-1972) lived nearly all of his life near Cholame (San Luis Obispo County) where his family has extensive land holdings in the Temblor Range. Shortly after his graduation from the University of California, Berkeley, he began cattle ranching activities, which he continued until his death.

In 1952 an outbreak of nitrate poisoning caused serious cattle losses in the Temblor Range, as well as other areas in California. Mr. Twisselmann wished to learn the identity of the plants causing the disease and this led to his serious interest in botany. He sought the help of John Thomas Howell and from Mr. Howell he learned the mechanics of collecting plants and the problems of identifying them. He first studied the plants of the Temblor Range and in 1956 published a flora of the area. His botanical horizon soon expanded to Kern County and in 1968 his flora of the county was published. Both of his floras list the plants, their local distributions, and their habitats but, because he had lived all of his life in the area of his floras and understood its ecology, he added from his observations the kind of information that could only come from personal experience and local sources. (For a bibliography of his writings see E. McClintock, *Fremontia* 1:3-4, 1973)

About 1965, with the cooperation of the United States Forest Service, Mr. Twisselmann began field work on the Kern Plateau in the southern Sierra Nevada of Tulare and Kern counties. He made a preliminary check-list, based on his collections together with those of J. T. Howell and Gordon True, which he planned to expand into a flora of the area.

During the years of his botanical activity Mr. Twisselmann built up a personal herbarium of about 20,000 specimens. In addition to his own collections others were acquired from local correspondents, mostly neighboring ranchers, who supplied him with material from their areas. Specimens in his herbarium were mounted in a professional fashion and he prepared for them specially designed and neatly printed labels. His herbarium was deposited in the Academy Herbarium.

Through his intensive collecting Ernest Twisselmann turned up several new species. Two named in his honor are *Nemacladus Twisselmannii* J. T. Howell and *Eriogonum Twisselmannii* (J. T. Howell) Reveal.

PLANTAGO CORONOPUS IN THE PACIFIC NORTHWEST.—*Plantago coronopus* L., a European species with distinctive pinnatifid leaves, has been established in California and at Port Orford, Oregon for many years (Munz, *A California flora*, 1959; Peck, *Manual of the higher plants of Oregon*, 1941). It was not included in recent floras of the Pacific Northwest (Hitchcock et al., *Vascular plants of the Pacific Northwest*, 1959; Hitchcock and Cronquist, *Flora of the Pacific Northwest*, 1973), although Abrams and Ferris (*Illustrated flora of the Pacific States*, 1960) reported it from Whidbey Island, Washington, and Linnton (Portland), Oregon. The presence of this species in Washington has been confirmed by a collection from Willapa Bay, 1 mi S Bay Center, Pacific County, Washington (Ganders 742, 18 Aug 1974, WTU and UBC). It was growing with a mixture of introduced weeds and typical maritime taxa such as *Convolvulus soldanella* L., *Grindelia integrifolia* DC. var. *macrophylla* (Greene) Cronq., *Lathyrus japonicus* Willd., and *Tanacetum douglasii* DC. *Plantago coronopus* is also known from a salt marsh at Ladysmith, Vancouver Island, British Columbia (*T. M. C. Taylor s. n.*, 13 Jul 1954, UBC).—FRED R. GANDERS, Department of Botany, University of British Columbia, Vancouver V6T, 1W5, Canada.

NOMENCLATURAL NOTES ON *TOWNSENDIA*.—In the excellent monograph of *Townsendia* by Beaman (Contr. Gray Herb. 183:1–151. 1957), the author, date, and place of publication for *T. condensata* are given as “D. C. Eat. in Parry, Am. Nat. 8: [106 ncm. nud.] 213. 1874”. The name was not validly published there according to part 2 of Article 34 of the *International Code of Botanical Nomenclature* (Regnum Veg. 82:40, 1972). Eaton stated, “Not having seen a specimen of Nuttall’s *T. incana*, I have some doubt as to whether this may not be his plant of that name. If not, it may properly bear the name which Dr. Parry has proposed.” The name must date from 1880 when Gray accepted the species and referred to Eaton’s description. The correct citation is: *Townsendia condensata* Parry ex Gray, Proc. Amer. Acad. Arts 16:83. 1880.

The author, date, and place of publication for *T. montana* is given in Beaman’s monograph as “M. E. Jones, Zoe 4:262. 1893”. The name was not validly published there according to Article 34, since Jones stated, “Other forms that may eventually prove to be *T. scapigera* I have given the provisional name of *T. montana*.” This name appears not to have been validated before Piper’s description of *T. alpigena*. The correct name for the species is: *Townsendia alpigena* Piper, Bull. Torrey Bot. Club 27:394. 1900. The following new combination is therefore necessary: *Townsendia alpigena* Piper var. *minima* (Eastwood) Dorn, comb. et stat. nov.—

T. minima Eastwood, Leaf. W. Bot. 1:206. 1936—*T. montana* Jones var. *minima* (Eastwood) Beaman, Contr. Gray Herb. 183:85. 1957.

—ROBERT D. DORN, Department of Botany, University of Wyoming, Laramie 82071.

SENECIO GANDERI: A UNIQUELY ADAPTED HERB FROM SOUTHERN CALIFORNIA.—The herbaceous perennial *Senecio ganderi* Barkley & Beauchamp (Brittonia 24:106. 1974) is known from only three isolated localities in southern San Diego County, California: at the head of two adjacent canyons on the north facing slope of Tecate Peak, the north facing slope of the east ridge of Lawson Peak, and the north east slope of El Cajon Mountain. Although *S. ganderi* occurs on recently burned sites at these localities, it has developed most extensively beneath the canopy of an unburned section of chaparral at the Lawson Peak site. This stand of chaparral, which has not burned in over 90 years, is free from any obvious unnatural disturbance (including grazing). The extensiveness of the population is in contrast to the well known characteristic lack of an herbaceous understory in chaparral. To quantify this shrub-herb relationship, cover data for shrubs and herbs were taken from two 100 m line transects placed perpendicular to each other in the middle of the Lawson Peak site in the spring of 1973. On the first line transect under a shrubby canopy of 82.5 percent (ground surface covered), composed predominantly of *Arctostaphylos glauca* and *Quercus dumosa*, there was an herbaceous layer of 33.6 percent (29.6 percent *S. ganderi* plus 4.0 percent others). On the second transect under a shrubby canopy of 87.8 percent, composed mainly of *Arctostaphylos glandulosa* and *Adenostoma fasciculatum*, there was an herbaceous layer of 34.7 percent (20.0 percent *S. ganderi* plus 14.7 percent others). In addition to this extensive occurrence of *S. ganderi*, abundant flower production by these plants attests to their being well adapted to conditions under mature chaparral.—JON. E. KEELEY, Department of Botany, University of Georgia, Athens 30602.

AN INTERSECTIONAL HYBRID IN *CEANOTHUS*.—Nobs (Publ. Carnegie Inst. Wash. 623. 1963) attempted a number of intersectional crosses in *Ceanothus*. Most of these failed completely, no hybrid seeds being formed. In rare instances a few hybrids were obtained but these were weak and stunted and died in early stages. Nobs cited only six naturally occurring intersectional hybrids in *Ceanothus*, none of which involved the putative parental pair reported here.

In 1970, Dr. Nancy Vivrette discovered an apparent hybrid between *Ceanothus* (sect. *Ceanothus*) *spinosus* Nutt. and *C.* (sect. *Cerastes*) *crassifolius* Torr.: California, Santa Barbara County, Santa Ynez Mountains, 0.16 km S of East Camino Cielo on Painted Cave Road. Voucher specimens of the hybrid and its putative parents are placed in UCSB. The hybrid grows between plants of the putative parents and is in such close proximity to the putative parents that their branches overlap. Nearby plants of both parental species are fully mature and vigorous, reaching heights of ca 3.5 m. The hybrid is also vigorous and stands ca 2 m. The hybrid is similar in some morphological characters to the putative parents and is intermediate in others (Table 1).

TABLE 1. SALIENT MORPHOLOGICAL CHARACTERS OF *CEANOTHUS SPINOSUS*, *C. CRASSIFOLIUS*, AND THEIR HYBRID.

character	<i>C. spinosus</i>	hybrid	<i>C. crassifolius</i>
Leaf shape	elliptical	elliptical to ovate	spatulate, obovate
Leaf texture	flexible	flexible	firm
Leaf dentation	none	dentate	pungently dentate
Leaf arrangement	alternate	alternate and opposite	opposite
Stipule texture	thin	thin	corky
Stem color	green	green and gray	gray
Branching habit	flexible	smallest branchlets flexible; larger branchlets rigid	rigid
Stomatal crypts	absent	present	present
Stomatal crypt pubescence	—————	minutely puberulent	tomentose
Position of inflorescence	lateral simple panicles	raceme of umbels	lateral umbels
Flower color	blue	light blue	white

The putative parents flower annually, set large numbers of seeds, and have 90 percent or higher pollen stainabilities (lactophenol-aniline blue). The hybrid has been observed for two years; very few inflorescences have been produced during that time. No seeds have been found on the hybrid; pollen stainability is 8.3 percent.—LAURIANNE L. HANNAN, 256 Wilson Street, Albany, California 94710.

CHROMOSOME NUMBER IN *MUILLA MARITIMA* (TORR.) S. WATS.—Lenz (Aliso 6:81–82, 1966) reported the somatic number of chromosomes as $2n = 20$ in *Muilla maritima* from Los Angeles County, California. Chromosome counts are now available for two collections of this species growing at the University of California Botanical Garden in Berkeley. One was collected by Wayne Roderick at Boyes Hot Springs, Sonoma County, California (U.C.B.G. accession 63.1296). The other was collected by Glen Keator ca one mile north of turn-off to Bunker Hill Road on highway 35 near Crystal Springs Reservoir, San Mateo County, California (U.C.B.G. accession 67.1243). Each has seven pairs of chromosomes at first metaphase in pollen mother cells. Two pairs are definitely smaller than the other five. Drawings of the metaphase chromosomes have been attached to vouchers in JEPS.

In a study of the embryology of this species, Berg and Maze (Madroño 18:143–151, 1966) stated that their findings do not support a close relationship of *Muilla* with other members of Allieae to which it is assigned. Chromosome numbers reported lend support to their opinion, since the most frequent numbers occurring in Allieae are $n = 8$ and 9 . The possibility that the $2n = 20$ found by Lenz could come from a triploid form is suggested.—MARION S. CAVE, Department of Botany, University of California, Berkeley 94720.

NOTES ON *ARCTOSTAPHYLOS GLAUCA* LINDL. VAR. *PUBERULA* J. T. HOWELL.—*Arctostaphylos glauca* var. *puberula*, which differs from typical *A. glauca* in its glandular pubescent to glandular hirsute or finely pubescent branchlets rather than glabrous and glaucous branchlets, has been reported at scattered localities from Santa Clara Co. to Ventura Co., California (McMinn, H. E., *An illustrated manual of California shrubs*, 1951). This variety is now being reported from several localities in southwest San Diego Co. The largest population is at the east end of Willows Road, The Willows. Specimens at this locality have glandular puberulent to glandular pubescent or glandular puberulent to nonglandular pilose branchlets, petioles, and leaf bases (*J. Keeley* 3200–3204, 3212–3218, 3301–3312). Specimens with similar types and amounts of pubescence have also been collected from Alpine Guard Station (*J. Keeley* 2949, 2952), Viejas Grade (*J. Keeley* 3221–3223), the junction of Lyons Valley Road and the Lawsen truck trail (*J. Keeley* 2889, 3317) and the south end of Boulder Creek Road (*J. Keeley* 3308). All specimens will be deposited in SD. At the Willow Road site this variety appears to intergrade with the type variety as all degrees of pubescence are found. In addition three observations suggest the hypothesis that hybridization with *Arctostaphylos glandulosa* Eastw. may be the source of variation at this locality. Three specimens had inflorescence bracts 4–7 mm long, twice that typical for *A. glauca*. This characteristic was also found in at least one individual from the Alpine, Viejas Grade, and Boulder Creek localities. Even more convincing however were the characteristics of the fruits from the Willow Road population. Rather than the smooth solid endocarp typical of *A. glauca*, many were ridged and channelled, some even breaking into distinct nutlets. Several individuals from the Lyons Valley-Lawson truck trail site also exhibited this characteristic. Both of these traits, i.e., large bracts and fruits that break into distinct nutlets, are characteristics of *A. glandulosa*, a shrub found in close association with *A. glauca* at all the localities cited above. In addition a small collection of fruits from *A. glandulosa* at the Willow Road site revealed several that were fused into solid stones. Although these characteristics may have arisen from hybridization, the two populations of *Arctostaphylos* species appear to be quite distinct in such major distinguishing characters as burl formation, glaucous leaves, fruit size, and shrub aspect.—JON E. KEELEY, Department of Botany, University of Georgia, Athens 30602.

LITERATURE OF INTEREST

Grasses in California. By B. Crampton. 178 pp. University of California Press, Berkeley. 1974. \$3.95 (paperback). Keys, descriptions, and illustrations of most common California grasses.

Sierra wildflowers: Mt. Lassen to Kern Canyon. By T. F. Niehaus, 223 pp. University of California Press, Berkeley. 1974. \$3.95 (paperback). Keys, diagnoses, and illustrations of most common species.

Introduction to California plant life. By R. Ornduff. 152 pp. University of California Press, Berkeley. 1974. \$3.95 (paperback). A discussion of California plant communities, including their origins, adaptations, and responses to environmental factors.

Native shrubs of the Sierra Nevada. By J. H. Thomas and D. R. Parnell. 127 pp. University of California Press, Berkeley. 1974. \$3.95 (paperback). Descriptions and illustrations of most common species.

The boojum and its home. By Robert R. Humphrey. 214 pp. University of Arizona Press, Tucson. 1974. \$6.95. A treatise on the ecology and natural history of *Idria columnaris* in Baja California.

The distribution of forest trees in California. By J. R. Griffin and W. B. Critchfield. 114 pp. Illustrated. Research Paper PSW-82/1972. Pacific Southwest Forest and Range Experiment Station, USDA, Forest Service, P.O. Box 245, Berkeley, California 94701. \$1.75.

Natural vegetation of Oregon and Washington. By J. F. Franklin and C. T. Dryness. viii + 417 pp. Illustrated. General Technical Report PNW-8. Pacific Northwest Forest and Range Experiment Station, USDA, Forest Service, Portland, Oregon. \$7.45. A revision of *Vegetation of Oregon and Washington* prepared for the XI International Botanical Congress in Seattle, 1969.

REVIEWS

Coastal ecology, Bodega Head. By MICHAEL G. BARBOUR, ROBERT B. CRAIG, FRANK R. DRYSDALE, and MICHAEL T. GHISELIN. 338 pp., 89 figs., 15 tables, 2 appendixes. University of California Press, Berkeley. 1973. \$10.95.

Coastal ecology, Bodega Head consists of eight short chapters covering parts of the history, some of the ecological research, and descriptions of the rocky, muddy, and sandy seashore communities and grassy headlands of Bodega Head, a small peninsula on the Pacific Coast 72 km (45 miles) north of San Francisco. The last part of the book contains checklists of Bodega Head plants and vertebrates, descriptions of methods used, a selected bibliography, and a literature cited section.

Although the title implies a general treatment of coastal ecology, the book is concerned primarily with Bodega Head, and appears only haphazardly to touch upon other coastal areas or to discuss fundamental processes or principles of coastal systems. The authors often digress, taking the reader off on asides that are usually interesting, but just as often questionable as to how they relate to coastal ecology or Bodega Head.

A segment of the general public, visitors to the region, nature lovers, and professional biologists would be interested in Bodega Head biology, and yet, the book appears to possess shortcomings when any of these audiences are considered. Many descriptions of organisms or communities were written without apparent attempts at simplification or organization, or regard for the kind of presentation necessary for comprehension by the novice, but are near nothings when examined by the professional looking to expand his knowledge in this area. The numerous little physiolog-

ical projects presented are also disconcerting, since in most cases, the results of small pilot studies, single samples, one instance, a set of readings, or incomplete information are presented in graphic or tabular form as substantial data, where it can only be misleading to the novice and distasteful to the professional.

Several academic questions are pursued, such as the community concept, zonation, the individualistic hypothesis, climax concept, and the like, which can only cloud the minds of the general reader attempting to learn about Bodega biology, while contributing nothing new to the thinking of professional biologists.

Discussions and topics that I looked forward to were often neglected or deficient. An interesting Indian history of Bodega Head (Chapter 7), and all the details of planning an atomic power plant at Bodega Bay are presented, while neglecting to develop a meaningful vegetational history, which I believe to be more pertinent to the understanding of present-day Bodega Head. I was disappointed that the questions of why Bodega Head is treeless, how long coastal grasslands might have been in existence, how coastal grasslands might have been formed and what factors contributed to their maintenance, and the possible relationships between the geomorphology and fault zone to soils, seepage, drainage, and vegetation were not discussed.

The role of salinity in controlling the germination of coastal plants, already, capably described in several publications by author Barbour, is emphasized to the point of neglecting other important aspects of coastal ecology, including wave action, sand transport, dune formation, dune-building plants, and the life cycle and ecological roles of the strand and salt marsh. What effects has the introduction of the non-native beachgrass had on Pacific Coast dunes, what native plants have been excluded, and how has this affected dune dynamics?

Along with the expected misspellings of Latin names, misuse of terms (I believe coastal strand should include the lower, middle, and upper beach, including the dunes), and misrepresentations of facts (common and snowy egrets may eat similar foods, but certainly procure them in different ways), many ecological features were neglected such as the role of runoff in removing salts, the effects of fresh-water seepage on beach plants, the ameliorating effects of marine air, and the reproductive habits of various plants and animals (sea rocket fruits are produced in pairs, with one abscising and the other persisting, thereby helping to explain why most seedlings are found near parent plants).

The various appendixes, and the literature cited section, are of use to both amateur and expert. The reader will encounter interesting ideas and facts, but I am afraid the book generally represents a premature venture as a comprehensive treatise of coastal ecology or of Bodega Head.—RICHARD J. VOGL, Department of Biology, California State University, Los Angeles 90032.

Flora of the Pacific Northwest: An illustrated manual. By C. LEO HITCHCOCK and ARTHUR CRONQUIST. Illustrated by Jeanne R. Janish. xix + 730 pp. University of Washington Press, Seattle. 1973. \$19.50 (text), \$25.00 (trade).

This manual, a direct outgrowth of the five-volume *Vascular plants of the Pacific Northwest*, has been most welcomed by both professional and amateur botanists of the Pacific Northwest. At last we have a reasonably sized, illustrated compendium of the plants of this area. The illustrations unfortunately have been greatly reduced from those found in larger work; however, they do provide an accurate visual guide for the enthusiastic plant identifier. Many new sketches have been provided for the keys, and even more would be desirable but I am sure that overall size of the manual precluded their inclusion. The presence of the illustrated keys provides for the first time in North America an excellent model for presentation in major floristic works. This unique feature will entice many more people to learn about our vascular plant resources. One problem the user has with the illustrations concerns the man-

ner in which they are related to the key leads rather than the species number. Perhaps a more distinctive separation of key lead numbers and species numbers should have been devised. One has the feeling that the illustrations are trying to serve two purposes and this leads to some confusion by the user.

The preliminaries contain a short introduction, a list of abbreviations and signs used, and a glossary. A separate list of abbreviations and signs is provided, but I have long since lost mine during field work. It is too bad that this list could not have been printed on the end papers. The glossary is adequate; however, I prefer it with back matter.

We have had the opportunity to use the manual both as a class text and as a research field tool during the past year and have found it to be most satisfactory. The keys obviously reflect the intimate experience that both authors have had with the plants in the field. Perhaps the most difficult aspect for the beginner, the terminology, is made more difficult by the need to abbreviate.

There have been some taxonomic changes and modifications from the previous five-volume work. New combinations are indicated in the index. Some changes are made without comment, e.g., reversal of *Antennaria microphylla* Rydb. and *A. rosea* Greene; *Sparganium emersum* Rehmann for *S. simplex*; the dropping of the B author of an A ex B authority that was used in the five-volume work, a procedure contrary to recommendations of the Code, e.g., *Picea engelmannii* Parry ex Engelm. and *Epipactis gigantea* Dougl. ex Hook. Three of the ten "new combinations" were made earlier by Boivin. It is hoped that the authors will publish a short paper bringing together the changes and providing their reasons for doing so.

I concur with the discussion provided by the authors regarding common names and support in particular the position taken by Hitchcock. I would, however, find it difficult to provide common names for species of *Carex* and wonder if it is not more confusing than clarifying.

Mention should be made of the printing of two text editions, namely, a trade edition with an elegant jacket (and a good picture of both authors!) that sells for over five dollars more than the text edition. I fail to see why the publishers have gone to the trouble of producing two different editions. Once again, as was the case with the previous five-volume work, the manual (text) is not well-bound. My edition is now in need of binding after a normal year's use in the laboratory and field. The University of Washington Press should be chastized for the sloppy way they have produced what is certainly one of North America's best conceived floristic works. I would hope in the future that the quality of the production would more nearly approach the scholarly content contained in the texts produced by Hitchcock and Cronquist.—ROY L. TAYLOR, Botanical Garden, University of British Columbia, Vancouver, Canada V6T 1W5.

A flora of the Tahoe Basin and neighboring areas. By GLADYS L. SMITH. 231 pp., 29 ill., 4 maps. Published by University of San Francisco in *The Wasmann Journal of Biology*, vol. 31, spring, 1973. Reprints with paper cover available from author: 730 - 28th Ave., San Francisco, CA 94121. \$5.85 (including postage and tax).

This flora is the culmination of 13 years of field and herbarium studies carried out by the author between 1959 and 1972. The flora covers an area of about 673 km² (260 mi²) in the Sierra Nevada within parts of six counties in the vicinity of Lake Tahoe on the California-Nevada border. Elevations in the area range from 1,926 m (6,320 ft) at Lake Tahoe to 3,317 m (10,881 ft) at Jobs Sister Peak. Aquatic vascular plants from Lake Tahoe itself are also included. In all, 1,161 taxa representing 903 species and 258 infraspecific taxa, distributed in 307 genera and 77 families, are treated.

The first 45 pages of the flora are devoted to a description of the study area and a survey of the history of botanical exploration in the region. Included are details of physiographic and geological features, a listing of plant communities with a floristic analysis, and a partial check-list of plants that occur on the summits of five or more peaks both east and west of the Sierran crest. This section is illustrated with 29 black and white photographs, of good quality, depicting various habitats and features of the area. Also provided are four line drawing maps, adapted from U.S. Geological Survey maps, of the study area. The study is supported by some 3,000 herbarium specimens collected by the author and deposited at JEPS and by "several thousand specimens representing the work of . . . collectors, ranging over a period of 112 years". These are located in four major San Francisco Bay Area herbaria.

The remainder of the flora consists of a catalogue of vascular plants arranged alphabetically by genera, which, in turn, are listed under families arranged in a modified Englerian sequence. For each taxon treated, the scientific name is followed by a common name, a statement concerning location and distribution, and a list of specimen citations together with their herbarium locations. Synonyms, as found in major West Coast floras, follow specimen citations, along with type locality information for taxa originally described from the area. Some of these type localities appear, however, to lie outside the area delimited by the author. In a few instances taxa are included on the basis of statements made by other workers, although the author has seen no specimens. Many comments and notes on various matters such distribution, distinguishing features, poisonous or edible qualities, etc., are added.

The text is relatively free of errors, and the print is easy to read. No keys or basic descriptions of taxa are given, however, making the work more of value as a reference than as a field guide.—KINGSLEY R. STERN, Department of Biological Sciences, California State University, Chico 95926.

A flora of the White Mountains, California and Nevada. By ROBERT M. LLOYD and RICHARD S. MITCHELL. viii + 202 pp., illustrated with nine black and white photographs and one map. University of California Press, Berkeley. 1973. \$8.00, buckram.

To many people the White Mountains, lying east of the southern end of the Sierra Nevada, are best known because of the old stands of bristlecone pine, *Pinus longaeva* Bailey. But there is much more there besides the pine: the White Mountains have been the site of much interesting ecological work and comprise an area of complex geology. The book contains a very good account of the vascular plants, a discussion of plant communities and vegetation (contributed by H. A. Mooney), a guide to the geology (contributed by V. C. LaMarche, Jr.), a history of botanical collecting, and a discussion of the plant geography and comparative floristics (written by the junior author).

In the section on plant communities, Mooney recognizes four major vegetation zones (desert scrub, pinyon woodland, subalpine forest, and alpine tundra) and discusses the more general features of each. Mitchell concludes (p. 35) that: ". . . the flora of the White Mountains presents the picture of a much depleted Pliocene flora surviving at mid-altitudes, superimposed by a northwestern flora at high altitudes, and encroached upon by warm-desert elements from below."

The White Mountains, some 2100 square kilometers in area and varying in elevation from about 1,220 to 4,342 meters, contain 76 families, 298 genera, and 811 specific and infraspecific taxa of vascular plants. The authors feel that their list is over 90 percent complete. The systematic section contains keys to families, genera, and species, distributional notes, localities, and specimen citations. It is unfortunate that specimens in a personal herbarium are cited. Editors of scholarly journals and books should insist that all cited material be in an established collection. We already

have enough cases of lost voucher material! Angiosperm families are arranged according to Cronquist's system of 1968 (*The evolution and classification of flowering plants*). Although much thought has gone into this phylogenetic sequence (which has stimulated even more thought), it seems pointless to this reviewer to arrange floras, especially local ones, which should be as easy to use as possible, according to one or another of the most recently proposed phylogenetic schemes. Why not stick to the "alphabets" we all know? One does not study local floras such as this generally excellent one to learn phylogeny.

The format is very pleasing and errors are few. One that will cause more amusement than confusion (p. 48) is the citation of Prof. LeRoy Abrams as the author of *Flora of the Pacific Northwest* instead of the *Illustrated flora of the Pacific States*.

One interesting aspect of this work is that it was done largely during the authors' spare time, during and after their graduate work at the University of California, Berkeley. This flora will be of great use to anyone dealing with the plants of the White Mountains and vicinity, and it is a distinct contribution to our understanding of the plant geography of California.—JOHN H. THOMAS, Department of Biological Sciences, Stanford University, Stanford, California 94305.

A flora of Southern California. By PHILIP A. MUNZ. viii + 1086 pp., map, 103 plates with some 600 figures. University of California Press, Berkeley. 1974. \$16.50.

No taxonomist has to be told why we need a new flora; but it is instructive to compare this one with the same author's *Manual of Southern California Botany*, published 39 years ago. The new book does cover the same plants, plus a few more; but how much more has been learned about them! (For just ten years' worth of additions and improvement, note the size of the supplement to Munz's *A California Flora*.) Yes, we need the new flora; and it is good that he finished it, even though he did not live to see it published.

Dr. Munz lived in southern California for about 55 years, first at Pomona College, where he became Professor of Botany and Dean of the Faculty, then, after an interim at the Bailey Hortorium of Cornell University, back at Rancho Santa Ana Botanic Garden, where he was Director until his retirement in 1960. He did extensive general collecting throughout California, but especially the southern part; and he was a steady and productive worker, turning out a series of books and monographs of high quality. He remained active beyond 80, as this new book clearly shows. And he was highly esteemed as a kind and gentle man, a good teacher, and a wise counselor.

The brief introduction to the book touches on the climate, vegetation, geology, and plant distribution in southern California—defined here as extending to Point Conception and Death Valley. The systematic treatment, according to the jacket blurb, covers more than 4000 species. Descriptions and keys are generally of the same scope and quality as those of *A California flora*, from which, in fact, they were largely taken—with necessary additions, subtractions, and improvements.

This book is most convenient for those who know the alphabet. Families are alphabetic under the main subdivisions and classes, which means mostly in two alphabetic sequences. Genera are alphabetic under families, species under genera, and, except for nominate taxa, subspecies and varieties under species. The family name heading the left-hand page and the generic on the right make finding easy, except that some of us may have to learn a few new family names—not Gramineae, for example, but Asteraceae, or whatever it is. The index also is alphabetic but might almost follow Dalla Torre and Harms, it is so nearly superfluous.

The specialist who knows one area or one family can always find details to criticize in a flora. (Perhaps we can criticize ourselves for not sending in those latest tidbits of information that must now await the next book.) However, it takes someone of broad knowledge to write a flora like this one: Dr. Munz was a specialist and monographer, yes; but he had breadth as well as depth.

Because of Dr. Munz's ill health, responsibility for proofreading was taken largely by non-botanists at the press, who have done well. I might search through for typographical errors and minor oversights and omissions to list, as some reviewers delight in doing; but everyone knows they occur in every book, and I would rather look at the work as a whole. To me it is a beautiful book—a boon to all of us, a final achievement in a long and productive career, and a memorial to an outstanding botanist and fine man, who will be missed by the botanical world and by all who knew him.—REID MORAN, Natural History Museum, St. Diego, Upper California 92112.

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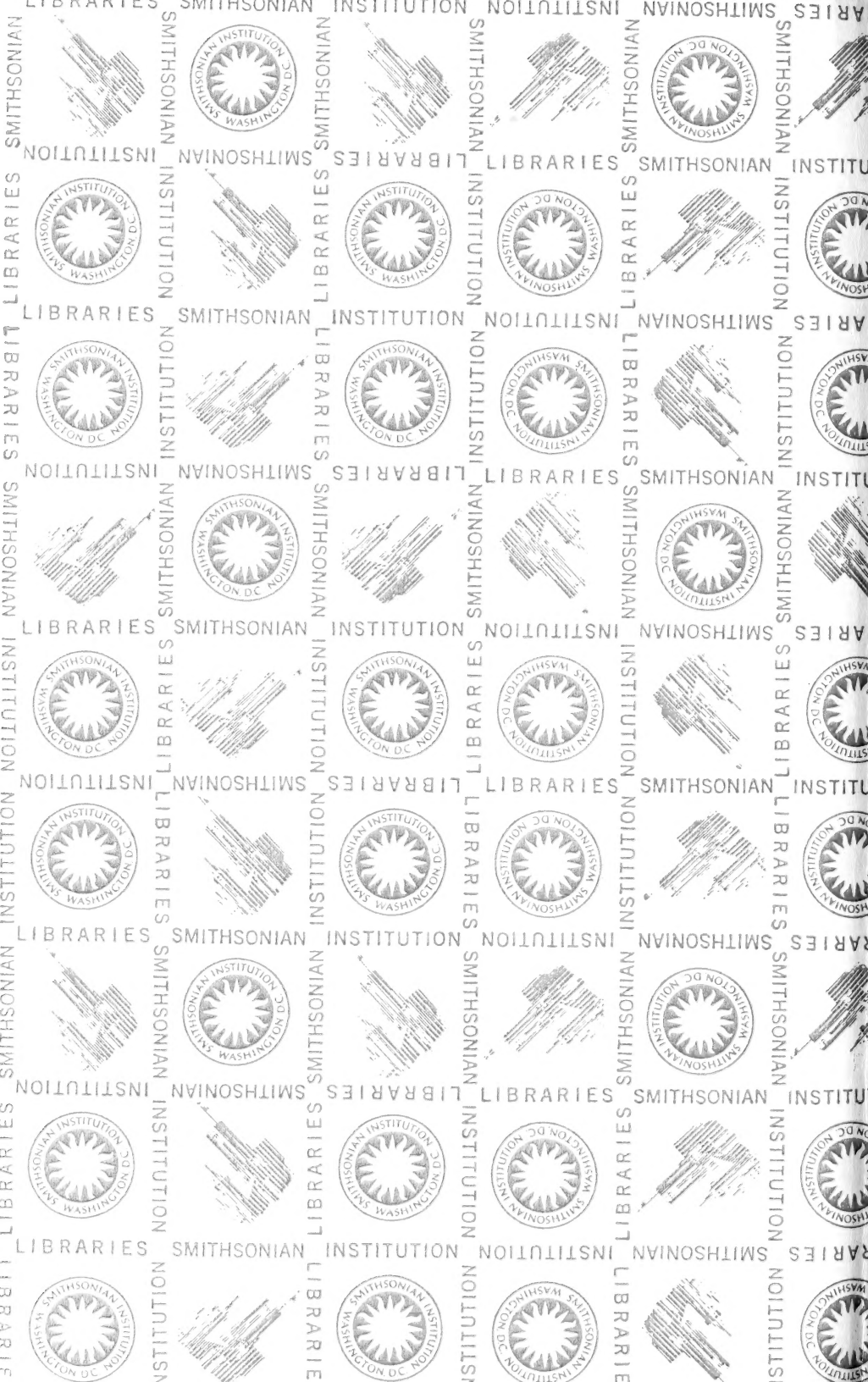
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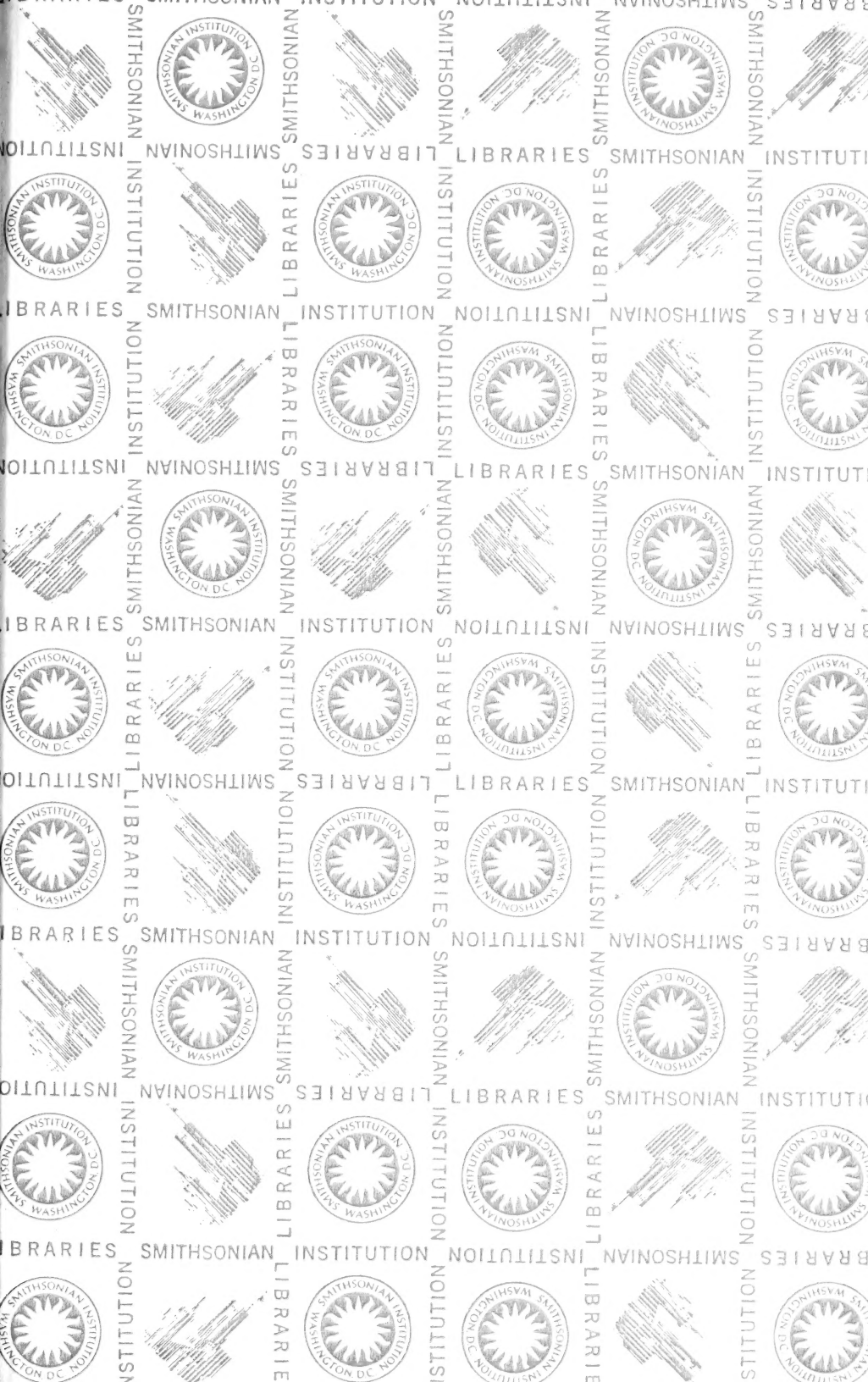
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